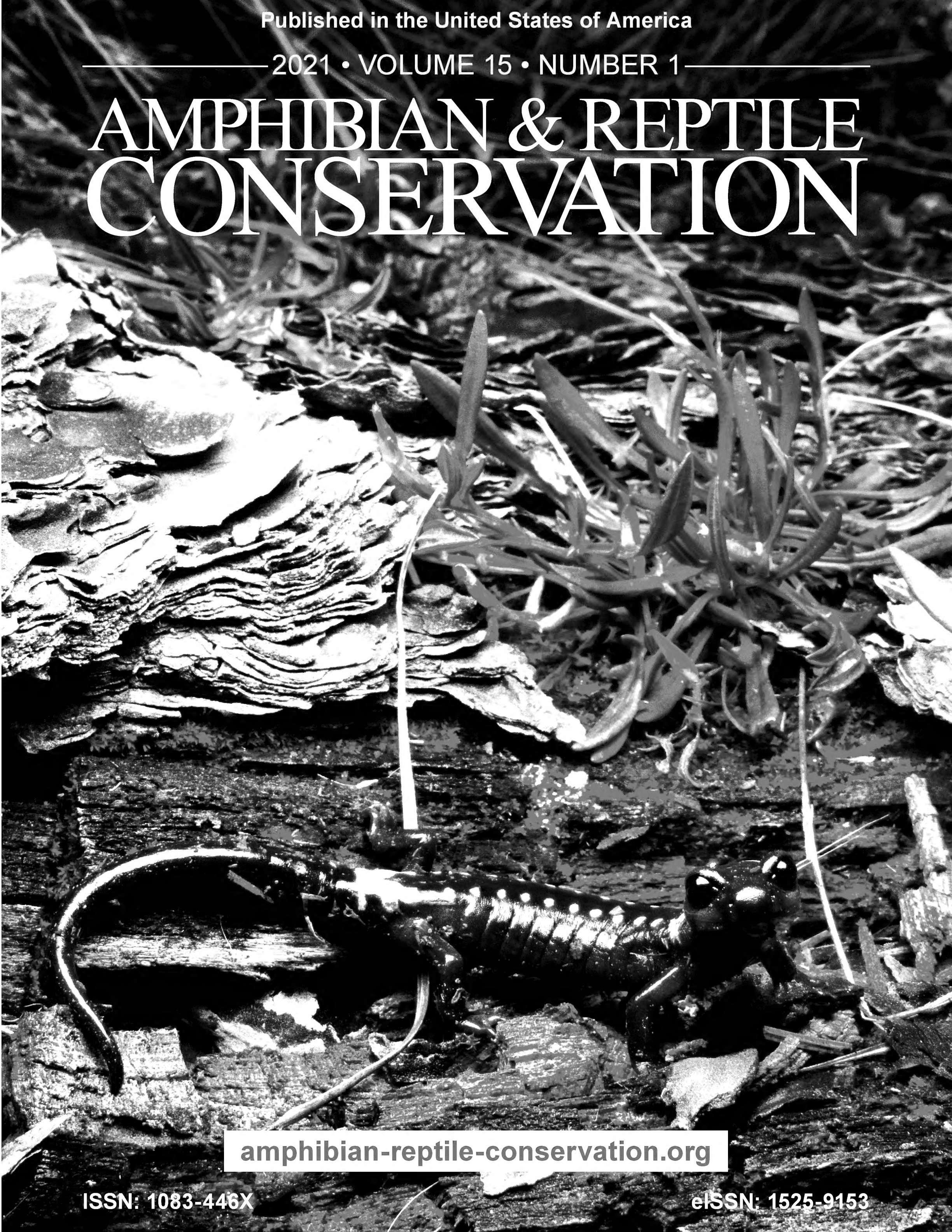


Published in the United States of America

2021 • VOLUME 15 • NUMBER 1

AMPHIBIAN & REPTILE CONSERVATION



amphibian-reptile-conservation.org

ISSN: 1083-446X

eISSN: 1525-9153



urn:lsid:zoobank.org:pub:9B3E8106-74E8-428F-B0BB-3CCD9EFDF0F3

Two new species of *Eleutherodactylus* (Anura: Eleutherodactylidae) from Southern Mexico, with comments on the taxonomy of related species and their advertisement calls

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Abstract.—An analysis of morphological and molecular data is presented here, as well as notes on advertisement calls from populations of the *Eleutherodactylus nitidus* species group (subgenus *Syrrophus*) from southern Mexico, and two new species are described based on the results. *Eleutherodactylus maculabialis* sp. nov. is unique among its congeners by a combination of characters including widely expanded finger tips, indistinct but visible inguinal glands, a dark venter, and conspicuous orange or pale cream spots present on the upper lip. *Eleutherodactylus sentinelus* sp. nov. is unique among its congeners by the combination of its advertisement call, smooth dorsal and ventral skin, and a unique combination of a brown dorsum, pale interorbital bar and mid-dorsal stripe, and bright yellow inguinal flash coloration. The molecular phylogenetic analysis indicates that both species are part of the *Eleutherodactylus nitidus* species group, and closely related to one another. Known collecting localities for both new species suggest they are restricted to small ranges in moist pine-oak woodland, cloud forest, and oak-tropical deciduous forest on the windward slopes of the Sierra Madre del Sur in Guerrero. We discuss the relationships of the new species to all the species in the *Eleutherodactylus nitidus* species group and the validity of some related taxa based on the results of our phylogenetic analysis. The male advertisement calls of the new species are presented graphically, along with those of the closely related species occurring in the Sierra Madre del Sur. Range maps are presented for all species of the *Eleutherodactylus nitidus* species group, as the group is currently understood.

Keywords. Amphibia, common names, conservation, Guerrero, phylogenetics, Sierra Madre del Sur

Resumen.—Presentamos un análisis de datos morfológicos, moleculares y de cantos de poblaciones del grupo *Eleutherodactylus nitidus* (subgénero *Syrrophus*) del sur de México y describimos dos nuevas especies basado en nuestros resultados. *Eleutherodactylus maculabialis* sp. nov. es única entre sus congéneres por una combinación de caracteres, incluyendo la punta de los dedos ampliamente expandida, la presencia de glándulas inguinales poco distinguibles y presentar coloración con un fondo oscuro y manchas naranjas o pálidas en el labio superior. *Eleutherodactylus sentinelus* sp. nov. es única entre sus congéneres por la siguiente combinación de caracteres que incluyen su canto de advertencia, piel lisa en el dorso y zona ventral y una combinación única de coloración dorsal café, una barra interorbital pálida, una línea a lo largo del dorso y una coloración inguinal amarillo brillante. El análisis filogenético molecular indica que ambas especies pertenecen al grupo *Eleutherodactylus nitidus*, y están cercanamente relacionadas. Las localidades de colecta conocidas para ambas especies sugieren que las mismas tienen una distribución restringida a pequeños rangos en bosques húmedos de pino-encino, bosque mesófilo de montaña y bosque tropical cauducifolio con encinos en las pendientes de la Sierra Madre del Sur de Guerrero. Discutimos la relación entre todas las especies asociadas al grupo *Eleutherodactylus nitidus* así como la validez de algunos taxones relacionados basado en nuestro análisis filogenético. Analizamos los cantos de advertencia de las nuevas especies y las especies relacionadas que ocurren en la Sierra Madre del Sur. Finalmente presentamos mapas de distribución de todas las especies del grupo *Eleutherodactylus nitidus*, ya que actualmente no se entiende bien dicho grupo.

Palabras clave. Anfibios, conservación, filogenética, Guerrero, Sierra Madre del Sur

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Two new *Eleutherodactylus* species from Mexico

Citation: Grünwald CI, Reyes-Velasco J, Franz-Chávez H, Morales-Flores KI, Ahumada-Carrillo IT, Rodríguez CM, Jones JM. 2021. Two new species of *Eleutherodactylus* (Anura: Eleutherodactylidae) from Southern Mexico, with comments on the taxonomy of related species and their advertisement calls. *Amphibian & Reptile Conservation* 15(1) [Taxonomy Section]: 1–35 (e272).

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Accepted: 6 November 2020; **Published:** 13 February 2021

Introduction

The frogs of the genus *Eleutherodactylus* Dumeril and Bibron, 1841 are among the most diverse and taxonomically challenging groups of amphibians in the New World (Hedges et al. 2008). The genus consists of five subgenera (Hedges et al. 2008), four of which are native to the West Indies (*Eleutherodactylus*; *Euhyas* Fitzinger 1843; *Pelorius* Hedges 1989; and *Schwartzius* Hedges et al. 2008), and a fifth (*Syrrhophus* Cope 1878), which is native to continental North America and Cuba. The native range of *Syrrhophus* extends from west-central Texas and central Sonora south through Mexico and into Guatemala and Belize, with two species in western Cuba. One species, *E. campi*, has been introduced to some urbanized parts of Texas (Dixon 2000), Louisiana (Hardy 2004), Alabama (McConnell et al. 2015), and Arizona (D. Ortiz, in press), presumably via the horticultural trade.

Whereas the systematics of the West Indian subgenera has been relatively well studied (Hedges et al. 2008), less attention has been given to the systematics of the subgenus *Syrrhophus* until recently. A recent effort by the authors sampled all of the currently recognized species of *Syrrhophus* in the United States, Mexico, and Guatemala. This resulted in Reyes et al. (2015) describing two distinctive new species of *Eleutherodactylus* from western Mexico based on mitochondrial DNA (mtDNA) sequence data, morphology, and advertisement calls.

In a continuation of that study, Grünwald et al. (2018) analyzed the morphological and molecular data of all known species within the subgenus, as well as the taxonomic history of *Syrrhophus*. That review led to the assignment of the continental North American species to two species series: the *Eleutherodactylus longipes* species series, which contains only the *Eleutherodactylus longipes* species group; and the *Eleutherodactylus nitidus* species series, which contains the *Eleutherodactylus nitidus* species group and the *Eleutherodactylus modestus* species group.

Those authors reviewed the *Eleutherodactylus modestus* species group in detail, describing six new species, synonymizing *E. nivicolimae* (Dixon and Webb, 1966) with *E. rufescens* (Duellman and Dixon, 1959), and providing data for the distinctiveness of *E. modestus* (Taylor, 1942), *E. pallidus* (Duellman, 1958), *E. teretistes* (Duellman, 1958), and *E. wixarika* Reyes-Velasco et al., 2015. Furthermore, those authors presented molecular evidence that *E. orarius* (Dixon, 1957) is distinct from *E. nitidus* (Peters, 1870). Recently, Palacios-Aguilar and Santos-Bibiano (2020) described a new species of saxicolous *Eleutherodactylus* from the lowlands of Guerrero, near the town of Tierra Colorada. With that

addition, there are currently 34 recognized species in the subgenus *Syrrhophus* in continental North America, plus two more in Cuba.

Here, we review the *Eleutherodactylus nitidus* species group in detail, and describe two more new species in that species group (*sensu* Grünwald et al. 2018) from the state of Guerrero. The morphological and molecular data for all named continental species of the subgenus *Syrrhophus* are analyzed to define the two new species. In addition, two subspecies are elevated to the species level and two other species are synonymized based on the results. These rearrangements result in 37 named species recognized as valid in the subgenus *Syrrhophus*, with (potentially) more awaiting description pending the completion of ongoing investigations.

Materials and Methods

Taxonomic sampling. From 2003–2019, the authors collected specimens of all known species of the subgenus *Syrrhophus* in Mexico, the United States, and Central America (Reyes-Velasco et al. 2015; Grünwald et al. 2018). Specimens of all currently recognized species of the subgenus (Frost 2020) were examined, and specimens of most species were measured, with the exceptions of *E. verruculatus* (Peters 1870) and the recently described *E. erythrochomus* (Palacios-Aguilar and Santos-Bibiano 2020). Comparisons of the new species described herein with the recently described species used the photos and data provided by the authors in the description (Palacios-Aguilar and Santos-Bibiano 2020). The validity of *E. verruculatus* has been questioned by various authors (Firschein 1954; Lynch 1970; Grünwald et al. 2018), and it is currently considered to be an enigmatic name with no known locality, genetic material, or recently collected specimens available.

All frogs were photographed alive—including dorsal, lateral, and ventral profiles, as well as photographs of each one showing the colors of flanks and flash colors on the groin and thigh. The frogs were euthanized with 10% ethanol or with topical benzocaine and tissue samples were obtained from thigh muscle or liver upon death and preserved in 96% ethanol. Specimens were preserved in 10% formalin and transferred to 70% ethanol for storage.

Measurements were taken from additional specimens of the subgenus *Syrrhophus* in the Museo de Zoología, Facultad de Ciencias (MZFC) of Universidad Nacional Autónoma de México (UNAM) and in the Amphibian and Reptile Diversity Research Center (ARDRC) of the

University of Texas at Arlington (UTA). Measurements were not taken directly for the type specimens of some previously described taxa so this study used the measurements of the type specimens provided in their original descriptions and published literature. Measurements of *Eleutherodactylus dilatus* (Davis and Dixon 1955), *E. fuscus* (Davis and Dixon 1955) (= *E. maurus*), and *E. albolabris* (Taylor 1943) are given in their original descriptions and in Dixon (1957a,b). Measurements for *E. nitidus* (Peters 1870) and *E. petersi* (Duellman 1954) were taken from Dixon (1957a,b), while measurements for *E. orarius* (Duellman 1958) and *E. syristes* (Hoyt 1965) were taken from their original descriptions. For *Eleutherodactylus pipilans* (Taylor 1940), *E. nebulosus* (Taylor 1943), and “*E. rubrimaculatus*” (Taylor and Smith 1945) this study used the measurements provided in their original descriptions and in Lynch (1970). Measurements of each of the above species were also taken from specimens collected during this study from the type localities or nearby.

The material collected is deposited at the Museo de Zoología, Facultad de Ciencias (MZFC) of the Universidad Nacional Autónoma de México (UNAM) in Mexico City. Specimen numbers for all material examined are provided in Appendix 1. While the specimens collected were formally catalogued at the MZFC, several of the examined specimens from both the MZFC and UTA collections have not been catalogued, and in such cases the original field numbers and their respective museums are listed.

Morphological measurements. The characters and terminology used herein follow those of Lynch and Duellman (1997), Savage (2002), and Grünwald et al. (2018). The following measurements were taken for each specimen (abbreviations listed in parentheses): snout-vent length (SVL); head length (HL); head width (HW); eyelid width (EW); interorbital distance (IOD); internarial distance (IND); eye-naris distance (END); diameter of eye (ED); width of tympanum (TW); height of tympanum (TH); eye-tympanum distance (ETD); upper arm length (UpL); forearm length (FoL); hand length (HaL); length of 1st finger (F1L); width of pad on 1st finger (F1PW); width of 1st finger (F1W); length of 2nd finger (F2L); width of pad on 2nd finger (F2PW); width of 2nd finger (F2W); length of 3rd finger (F3L); width of pad on 3rd finger (F3PW); width of 3rd finger (F3W); length of 4th finger (F4L); width of pad on 4th finger (F4PW); width of 4th finger (F4W); inner palmar tubercle length (IPTL); middle palmar tubercle length (MPTL); outer palmar tubercle length (OPTL); femur length (FeL); tibia length (TL); tarsal length (TaL); foot length (FL); total foot length (TotFL); length of 2nd toe (T2L); width of pad on 2nd toe (T2PW); width of 2nd toe (T2W); length of 3rd toe (T3L); width of pad on 3rd toe (T3PW); width of 3rd toe (T3W); length of 4th toe (T4L); width of pad on 4th toe (T4PW); width of 4th toe (T4W); length of 5th

toe (T5L); width of pad on 5th toe (T5PW); width of 5th toe (T5W); inner metatarsal tubercle length (IMTL); and outer metatarsal tubercle length (OMTL). Hand length (HA) was measured from the tip of the longest finger to the base of the palm, and foot length (FL) was measured from the tip of the longest toe to the base of the tarsus. The outer palmar tubercle refers to a small tubercle on the outer surface of the palm, but not one of the larger supernumerary tubercles. While these tubercles are usually present in *Syrrhophus*, they are generally absent in some species and their presence is variable in others.

Molecular analysis: DNA extraction and PCR amplification. A detailed description of the DNA extraction and PCR amplification protocols can be found in Grünwald et al. (2018). DNA was extracted from tissue samples using a standard potassium acetate protocol and a fraction of the 16s rRNA mitochondrial gene was sequenced using either the primers LX12SN1a (forward) and LX16S1Ra (reverse) of Zhang et al. (2013), or the modified primers 16Sar and 16Sbr of Bossuyt and Milinkovitch (2000). Unpurified PCR products were then shipped for sequencing to BGI Tech Solutions (Hong Kong).

Molecular analysis: sequence alignment and phylogenetic analysis. Regions with poor quality base calls were removed by manually trimming the 5' and 3' ends of all sequences using the program Geneious v6.1.6 (Biomatters Ltd., Auckland, New Zealand). All sequences were then aligned in Muscle (Edgar 2004), with a final alignment of 560 base pairs. Additionally, multiple sequences already available in GenBank were included. Two Cuban species of the subgenus *Syrrhophus* (*E. symingtoni* and *E. zeus*) were included as outgroups in the phylogenetic analysis. The final alignment included 104 individuals, of which 65 are new. All the new sequences have been deposited in GenBank and their accession numbers are shown in Appendix 2.

Bayesian inference of phylogeny (BI) was performed in MrBayes v3.2.2 (Ronquist et al. 2012), implemented on the CIPRES Science gateway server (Miller et al. 2010). First, the best-fit models of nucleotide substitution for the 16s rRNA mitochondrial gene were selected using the Bayesian Information Criterion (BIC) implemented in PartitionFinder v1.1.1 (Lanfear et al. 2012). The Bayesian analysis consisted of four runs of 10 million generations each, with four chains (one cold and three heated), and sampling every 1,000 generations. Tracer v1.6 (Drummond and Rambaut 2012) was used to confirm the convergence of the independent runs, based on overlap in likelihood and parameter estimates among runs, as well as effective sample size (ESS) and Potential Scale Reduction Factor value estimates (PSRF). PSRF indicated that individual runs had converged by 100,000 generations, so the first 25% of the runs were discarded as burn-in. Finally, posterior probability values were annotated on the

resulting topology using the program TreeAnnotator v1.8.3 (Rambaut et al. 2014). Additionally, genetic distances were obtained for the members of the group through the use of Mega X (Kumar et al. 2018).

Advertisement call graphing. Vocalizations were recorded for two individuals of each new species described here, as well as all other members of the *Eleutherodactylus* (*Syrrhophus*) *nitidus* species group (*sensu* Grünwald et al. 2018). The frogs were recorded while they were actively calling in the field, using the WavePad free recording software (NCH Software 2015) on various Apple iPhones. The calls were recorded at distances ranging from 50–150 cm, although distances within 100 cm of the frog were used whenever possible. Ambient temperatures were not obtained at the time of recording, but the time of day when each recording was made was noted.

The individual calls were isolated from other calls and background noise using Adobe Audition CC, and the calls were then analyzed using the software Raven Pro 1.5 (The Cornell Lab of Ornithology 2014). The Raven Pro settings were as follows: window size = 256 samples; window type = Hanning; overlap = 50%; DFT size = 256 samples; and grid spacing = 188 Hz. Temporal and spectral properties of isolated calls were analyzed using the Seewave version 1.6.4 package (Sueur et al. 2008) of the R statistical environment, version 3.3.2 (R Core Team 2016). Dominant frequency was estimated using a fast Fourier transform and fundamental frequency was estimated via short-term cepstral transform (Hanning window length = 256 samples with 80% overlap between successive windows for both spectral properties). 2D spectrograms were visualized using a sliding window analysis of short-term Fourier transform calculations.

Species descriptions. In order to simplify the identification of the two new species, their descriptions include comparisons of all the related species. To avoid confusion as to the point at which each species is formally described, the new species names are followed by “**sp. nov.**” until the point in the paper where a holotype is designated. Furthermore, for the sake of clarity the epithet “**sp. nov.**” is also used in the tables, figures, maps, appendices, and the molecular tree. The epithet “**sp.**” is used for the new species which are not described herein.

Results

Eleutherodactylus maculabialis sp. nov.

Spot-lipped Trilling Frog, *Rana trinadora* de labios manchados.

Figs. 1–2, 7A.

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Holotype. MZFC 33312 (CIG 00921). Adult male (Fig. 1), 11.4 km S of Puerto de Gallo, Municipality of Atoyac

de Álvarez (17.4672, -100.1916, datum = WGS84; 1,980 m asl), Guerrero, Mexico (Fig. 8A), collected on 15 July 2016 by Christoph I. Grünwald and Héctor Franz-Chávez.

Paratypes (*n* = 13; Fig. 2). MZFC 33307–311, 33313–314 (CIG 00916–920; 00922–923), seven adult males, collected at same locality and on same date as holotype; MZFC 33315–316 (CIG 00940–941), two adult males, 1.0 km S of bridge between Nueva Delhi and El Paraíso, Municipality of Atoyac de Álvarez (17.4150, -100.1924 datum = WGS84; 1,320 m asl), Guerrero, Mexico, collected on 15 July 2016 by Christoph Grünwald and Héctor Franz-Chávez; MZFC 33317–319 (CIG 00945–00947), two adult males, Yerba Santa, Municipality of General Heliodoro Castillo (17.5202, -99.9639, 2,003 m asl; datum = WGS84), Guerrero, Mexico collected on 16 July 2016 by Christoph Grünwald and Héctor Franz-Chávez; MZFC 33321 (CIG 00949), one adult male, 8.5 km N of Yerba Santa on road to Carrizal de Bravo, Municipality of General Heliodoro Castillo (17.5269, -99.9371, 1,880 m asl; datum = WGS84), Guerrero, Mexico, collected on 16 July 2016 by Christoph Grünwald and Héctor Franz-Chávez.

Diagnosis. Based on the phylogenetic analysis, this is a member of the genus *Eleutherodactylus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008). It is in the *Eleutherodactylus* (*Syrrhophus*) *nitidus* species series and the *Eleutherodactylus* (*Syrrhophus*) *nitidus* species group as defined by Grünwald et al. (2018) based on the condition of the tympanic annuli, ventral epidermis, and visceral peritoneum. A small frog, adult males measure 17.9–24.7 mm SVL; vocal slits are present in males, readily visible under partially translucent ventral epidermis; digital tips are expanded, 1.5–2.1 times the width of the narrowest part the finger on the third and fourth fingers; fingers moderately long, finger lengths are I-II-IV-III with third finger length ranging from 17–19% of SVL; compact lumbar gland above the inguinal region present, indistinct, barely visible in live specimen; ventral epidermis is partially translucent and visceral peritoneum is clear, not white, thus abdominal vein is not clearly visible against a white background on the venter of live specimens, and viscera are partially visible through translucent dark gray ventral epidermis; limbs moderate, TL/SVL ratio is 0.44–0.50, FeL/SVL ratio is 0.41–0.47 and TotFL/ SVL ratio is 0.66–0.73; snout relatively short, END/ SVL ratio is 0.10–0.12; tympanum small, indistinct and round, tympanic annuli not visible in live specimen; TW/ED ratio is 0.25–0.29. The dorsal, lateral, and ventral skin is smooth or slightly shagreen. Dorsal coloration variable, orange, tan, or brown, with darker brown marbling; loreal region dark brown, with conspicuous large white or orange spots present on upper labial region, and 1–3 orange spots on lower loreal region and upper portion of upper labia; pale interorbital

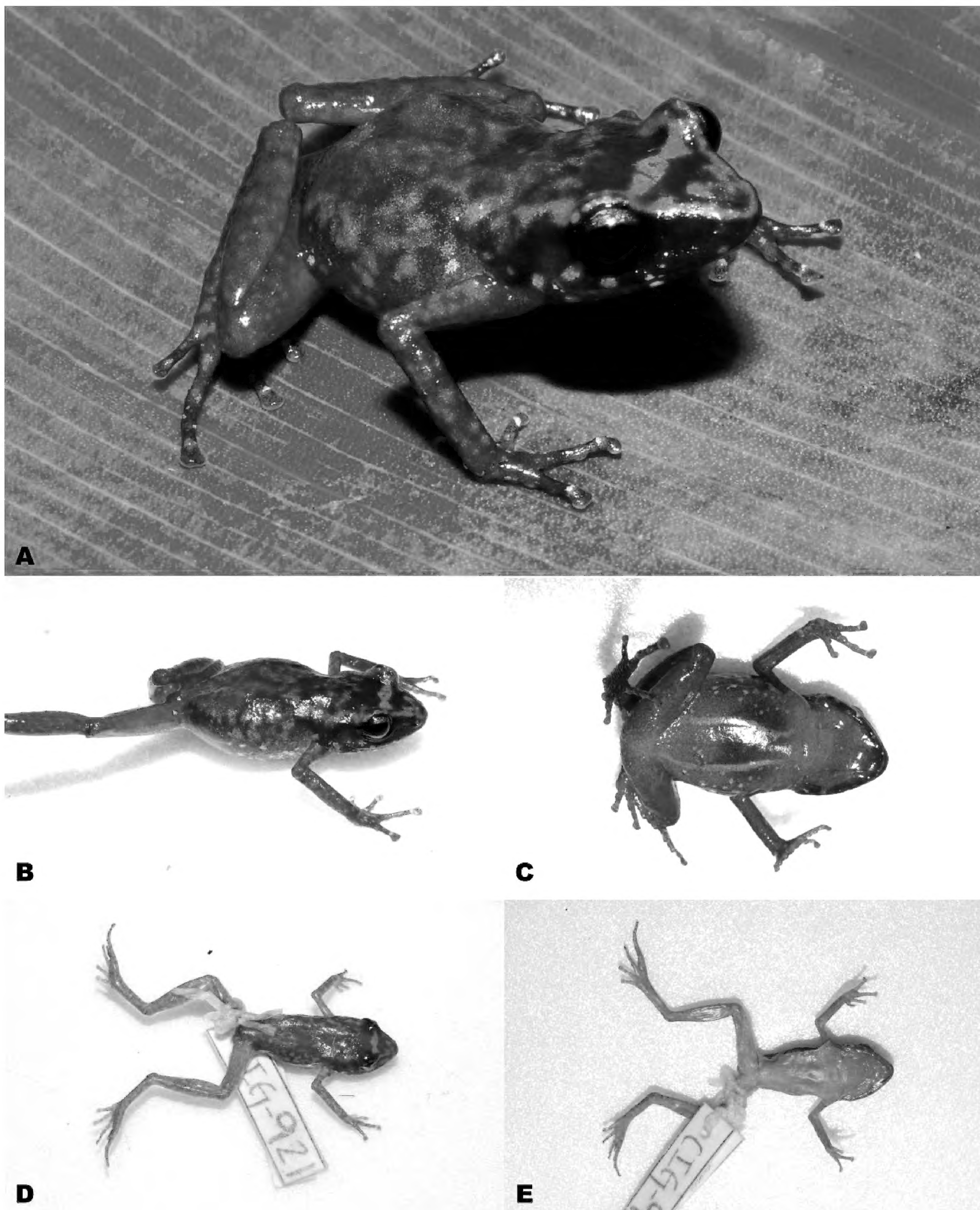


Fig. 1. Holotype of *Eleutherodactylus maculabialis* **sp. nov.**, MZFC 33312 (CIG 00921) from 11.4 km S of Puerto de Gallo, Municipio de Atoyac de Álvarez, Guerrero, Mexico. **(A)** Dorsolateral perspective in life. **(B)** Lateral perspective in life. **(C)** Ventral perspective in life. **(D)** Dorsal perspective in preservative. **(E)** Ventral perspective in preservative.

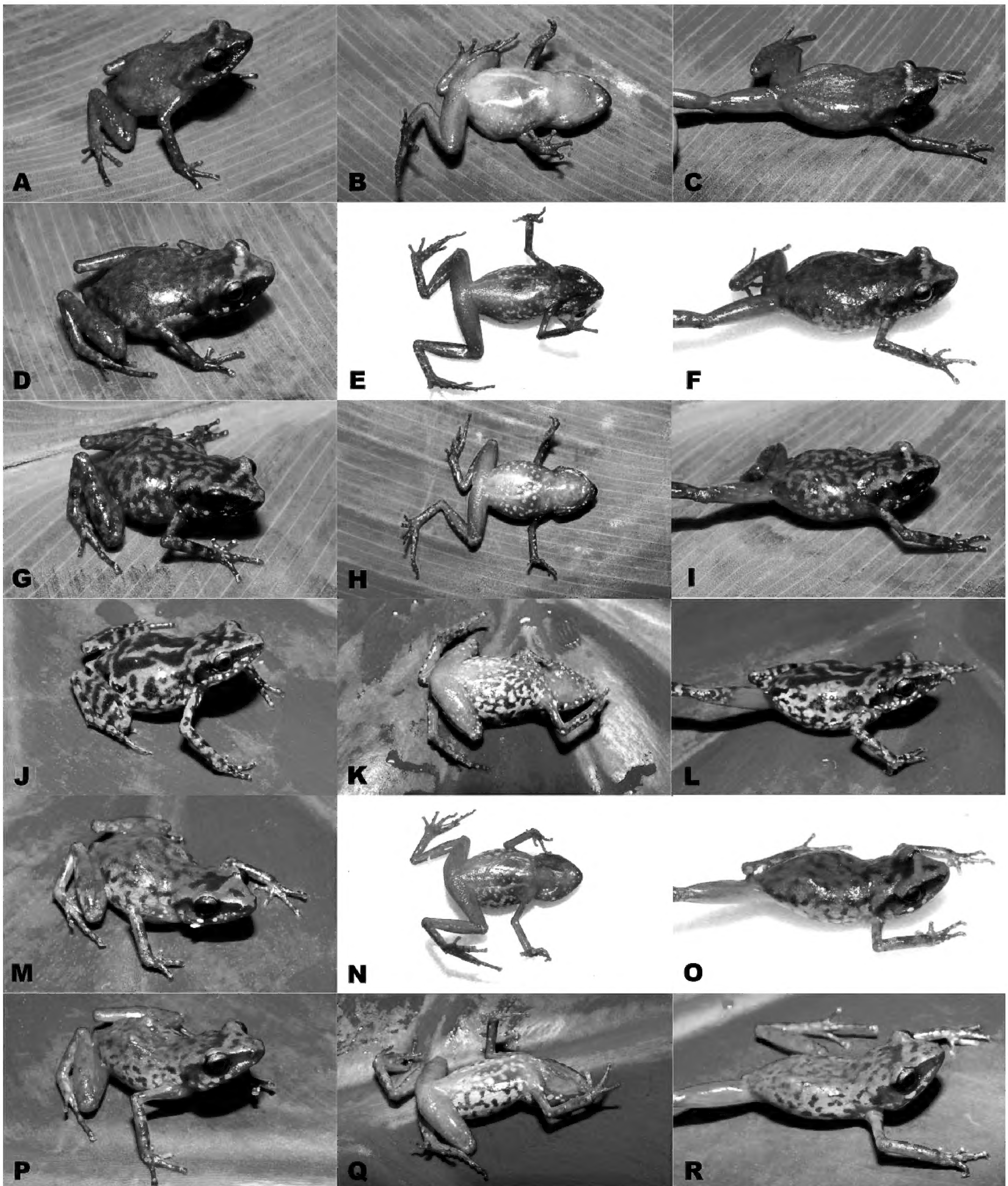


Fig. 2. Some of the paratypes of *Eleutherodactylus maculabialis* **sp. nov.** in life. (A–C) MZFC 33310 (CIG 00919); (D–F) MZFC 33311 (CIG 00920); (G–I) MZFC 33314 (CIG 00923) all from type locality; (J–L) MZFC 33321 (CIG 00949); (M–O) MZFC 33318 (CIG 00946); (P–R) MZFC 33317 (CIG 00945) all from the vicinity of Yerba Santa on road to Carrizal de Bravo, Municipality of General Heliodoro Castillo, Guerrero, Mexico.

bar present, orange or tan, same color as palest dorsal coloration; indistinct transverse bands present on legs; upper arms same coloration and pattern as forearms; no pale mid-dorsal stripe; upper flanks same color as dorsum, lower flanks lavender or gray with white spots and marbling; venter gray to dark gray with sparse white spots or marbling present. Red, reddish, or orange inguinal flash colors sometimes present on thighs and groin; however, when present these colors are not more vivid than the coloration of the light interorbital bar and the characteristic colored spots on the upper lip. The mating call of adult males is a short trill (see below; Fig. 3).

Comparisons. *Eleutherodactylus maculabialis* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* species series by: possessing a small, indistinct tympanum with no tympanic annulus visible and with a diameter less than 30% of diameter of the eye; by possessing a ventral epidermis which is not clear, and combined with a visceral peritoneum which is not white, an abdominal vein on the venter which is not clearly evident against a white background in life; and by possessing a distinct, raised lumbar gland above the inguinal region.

Eleutherodactylus maculabialis can be distinguished from species of the *Eleutherodactylus* (*Syrrhophus*) *modestus* species group by the combination of possessing a compact, protruding lumbar gland above

the inguinal region, digital tips which are expanded more than 1.5 times the width of the narrowest part the finger on the third and fourth fingers, and the presence of an interorbital bar.

Within its own species group, *E. maculabialis* can be distinguished from most species by possessing a compact inguinal gland that is indistinct but visible in live specimens. This character may or may not be visible in preserved specimens depending on how they were preserved. This species differs from *E. pipilans*, *E. erythrochomus*, and *E. nebulosus*, which lack a visible compact lumbar gland altogether. All other known species in the *E. (Syrrhophus) nitidus* species group have readily visible compact lumbar glands above the inguinal region. *Eleutherodactylus maculabialis* can be further distinguished from *E. pipilans* and *E. nebulosus* by possessing digital tips which are expanded more than 1.5 times the width of the narrowest part of the finger, and from *E. erythrochomus* by possessing digital tips which are more than 1.5 times but less than 3.0 times the width of the narrowest part of the finger. It may be distinguished from *E. nitidus*, *E. petersi*, and *E. orarius* by the combination of smoother skin, longer limbs, and tips of digits which are expanded more than 1.5 times the narrowest part of the finger on the third and fourth fingers. It is distinguished from *E. albolabris* by the following characters (characters of *E. albolabris* in parentheses): smaller size, 17.9–24.7 mm (23.0–26.8 mm), venter which is partially translucent and partially

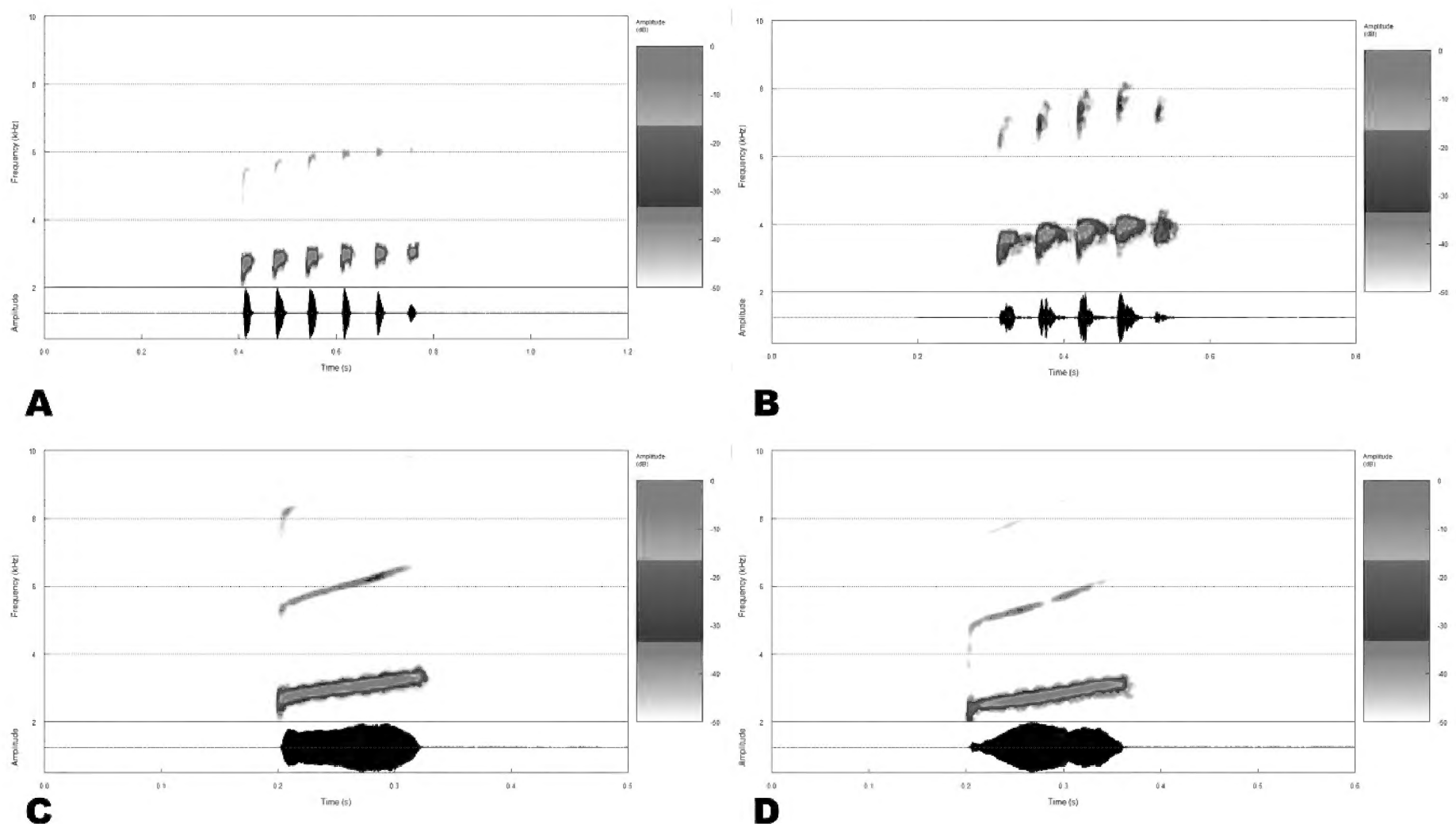


Fig. 3. Oscillograms and spectrograms of the advertisement calls of *Eleutherodactylus maculabialis* **sp. nov.** and *Eleutherodactylus sentinelus* **sp. nov.** (A) Adult male *E. maculabialis* **sp. nov.** from type locality. (B) Adult male *E. maculabialis* **sp. nov.** from 1.0 km S of bridge between Nueva Delhi and El Paraíso, Municipality of Atoyac de Álvarez, Guerrero, Mexico. (C) Adult male *Eleutherodactylus sentinelus* **sp. nov.** from Puerto El Balsamo, Municipality of José Azueta, Guerrero, Mexico. (D) Adult male *Eleutherodactylus sentinelus* **sp. nov.** from type locality.

white with black markings (entire venter white with black markings), pale longitudinal blotch absent in mid-dorsal area (pale mid-dorsal blotch usually present in mid-dorsal area), smaller tympanum with TW/ED 0.25–0.28 (larger tympanum with TW/ED 0.27–0.32). *Eleutherodactylus maculabialis* may be distinguished from *E. dilatatus* by the following characters (characters of *E. dilatatus* in parentheses): smooth dorsal and ventral skin (rugose), dark gray ventral coloration with white spots (white ventral coloration with dark gray marbling), conspicuous white or orange spots on labial region (dark labial region, sometimes with white or pale yellow speckling), flash color absent, or when present not brighter than the pale coloration on dorsum and head (bright yellow flash coloration in inguinal region). *Eleutherodactylus maculabialis* may be distinguished from *E. maurus* by the following characters (characters of *E. maurus* in parentheses): presence of pale interorbital bar same color as snout (no pale interorbital bar), dark gray ventral coloration with white spots (white ventral coloration with dark gray marbling), conspicuous white or orange spots on labial region (dark labial region, sometimes with white or pale yellow speckling), smooth dorsal and ventral skin (rugose or slightly rugose dorsal and ventral skin), no pale mid-dorsal stripe present and upper arms same color as rest of limbs (thick, pale brown mid-dorsal strip usually present and upper arms pale ground coloration, unmarked and lighter than other limbs). *Eleutherodactylus maculabialis* is most similar to *E. syristes*. Both species share smooth dorsal and ventral skin, distinct compact lumbar glands above the inguinal region which are variably marked, a variable dorsal coloration of orange, brown, or tan with darker marbling, and similar red, reddish, or orange flash colorations. *Eleutherodactylus maculabialis* may be distinguished from *E. syristes* by the following characters (characters of *E. syristes* in parentheses): digital tips expanded more than 1.5 times the width of the narrowest part the finger on the third and fourth fingers (digital tips which are expanded 1.1–1.5 times the width of the narrowest part the finger on the third and fourth fingers), ventral coloration dark, with pale orange or white spots (ventral coloration white, with dark gray or black marbling and reticulations), conspicuous white or orange spots on labial region (labial region dark, occasionally with light gray or white speckling). Furthermore, *E. maculabialis* differs from all species in its species group by its advertisement call, which is a short trill. The only other species in the species group which has an advertisement call that is a trill is *E. syristes*, but the call of that species is much more drawn-out (see below, Fig. 11A–B).

Description of the holotype. Male, relatively small (23.5 mm SVL); head longer (7.8 mm) than wide (6.9 mm), head slightly wider than body; snout subovoid from a dorsal view and rounded from a lateral profile;

tympanum indistinct, rounded with no supra-tympanic fold present; tympanum small, circular, greatest width of tympanum 0.7 mm; greatest diameter of eye 2.7 mm; tympanum width to eye diameter 0.27; eyelid width 1.5 mm, approximately 32% of the IOD, first finger shorter than second finger; finger lengths from shortest to longest I-II-IV-III with two and three equal; digital pads on fingers two, three, and four expanded, 1.9 times the narrowest point of the digit on fingers three and four; expanded finger pads slightly rounded, three palmar tubercles; inner palmar tubercle about 70% as large as middle palmar tubercle, outer palmar tubercle about 45% the size of middle palmar tubercle (Fig. 6A); toe lengths from shortest to longest I-V-II-III-IV, TL2 and TL5 very similar; outer metatarsal conical with a round base, moderate, approximately 66% of inner metatarsal tubercle; inner metatarsal tubercle spherical shape with oval base, large, approximately 0.9 mm in length. Dorsal skin smooth, lateral skin slightly shagreened, ventral skin smooth to slightly areolate. Skin was smooth in life. Vocal slits present.

In life the holotype had a reddish-tan dorsal coloration on the back (Fig. 1A–C), with darker brown mottling that was increasingly dense towards the mid-dorsal area. The pale orange was present on flanks, interorbital bar and spots on labial region. The flanks were reddish-tan with indistinct darker brown mottling and small white spots. The hind legs and arms were reddish-tan with irregular brown transverse bars. Bright reddish-orange flash colors on groin or thighs. Ventral coloration was gray with white and orange spots on throat and upper chest.

Coloration in preservative is light brown dorsum, with darker brown markings and a pale tan interorbital bar. The dorsal surfaces of the legs are light brown and the groin and posterior surfaces of the thighs are brown. The venter is white, with light brown on throat (Fig. 1D–E).

Measurements of the holotype (in mm). IND 2.5, IOD 4.8, END 2.5, ETD 0.9, UpL 6.3, FoL 7.5, HaL 5.5, F1L 1.8, F1PW 0.5, F1W 0.4, F2L 2.4, F2PW 0.7, F2W 0.4, F3L 3.9, F3PW 0.9, F3W 0.5, F4L 2.4, F4PW 0.8, F4W 0.4, IPTL 0.7, MPTL 1.0, OPTL 0.4, FeL 10.5, TL 11.5, TaL 5.9, FL 10.2, T2L 3.5, T2PW 0.8, T2W 0.5, T3L 4.6, T3PW 0.8, T3W 0.5, T4L 7.2, T4PW 0.9, T4W 0.5, T5L 3.1, T5PW 0.6, T5W 0.4, IMTL 0.9, OMTL 0.6, FeL/SVL 45%, TL/SVL 49%, Ha/SVL 23%, FL/SVL 43%, HL/SVL 33%, HW/SVL 29%.

Variation. SVL from 17.9–24.7 mm (21.65 ± 1.77). Expanded finger pads vary from 1.5–2.1 times the narrowest part of the digit on the third and fourth fingers, with average of 1.7 ± 0.21 on the third finger and average of 1.73 ± 0.21 on the fourth finger. Dorsal ground coloration ranged from different shades of tan, reddish, or brown, always with darker brown coloration

on the dorsum. Different degrees of dark mottling are present on the dorsal surfaces. Venter always gray, but with varying amounts of white spots. Characteristic bright orange spots on upper part of upper labial and lower part of loreal region present in most individuals (MZFC 33307–314); however, these spots may be faded or white in individuals from lower elevations (MZFC 33315–19, 33321), and one specimen (MZFC 33316) has only one pale spot on the right side, and none on the left. In some individuals, orange coloration may be lacking on the lip (MZFC 33315–19, 33321), in these individuals it is lacking everywhere, including the inguinal region and on the interorbital bar. Morphological variation is presented in Table 1.

Distribution and ecology. This species is known from two municipalities in the Sierra Madre del Sur of central Guerrero (Fig. 7A). It has been collected in tropical evergreen forest, cloud forest, oak woodland, pine-oak forest, and riparian vegetation between 900–2,100 m asl. All specimens were collected from low-growing vegetation or rocks along road cuts while calling in the month of July. This species has been collected in sympatry with *E. albolabris* and *E. nitidus*.

Etymology. From the combination of the Latin words *maculatus* and *labialis*, meaning spotted-lip, named for the conspicuous bright colored spots on the upper lip and above the rictus, present in varying degrees, which along with the advertisement call help to readily distinguish this species in the field.

Referred specimens. CIG 01484–01485, 01501, three adult males collected at the type locality on 29 June 2019 by Christoph I. Grünwald, Karen I. Morales-Flores, Janelle Morales-Flores; JAC 22216, one adult male, collected between Nueva Delhi and Puerto del Gallo, Municipality of Atoyac de Álvarez (17.4668, 100.198, 2,020 m asl, datum WGS84), Guerrero, Mexico on 15 June 2002 by Jonathan A. Campbell; JAC 25643–25646, four adult males, collected at Nueva Delhi, Municipality of Atoyac de Álvarez (17.4113, -100.1954, 1,239 m asl, datum WGS84), Guerrero, Mexico on 6 July 2004 by Jonathan A. Campbell.

***Eleutherodactylus sentinelus* sp. nov.**

El Balsamo Peeping Frog, *Rana piadora* del Puerto El Balsamo.

Figs. 4–5, 7B.

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Holotype. MZFC 33306 (CIG 00913). Adult male (Fig. 4), 8.9 km SW of Puerto El Balsamo, Municipality of José Azueta (17.9549, -101.2253, 1,354 m asl; datum = WGS84), Guerrero, Mexico (Fig. 8B), collected on 14 July 2016 by Christoph I. Grünwald and Héctor Franz-Chávez.

Paratypes ($n = 7$; Fig. 5). MZFC 33302–33305 (CIG 00907–910), four adult males, collected at Puerto El Balsamo, Municipality of José Azueta (17.9813, -101.2291, 1,900 m asl; datum = WGS84), Guerrero, Mexico on 14 July 2016 by Christoph I. Grünwald and Héctor Franz-Chávez; MZFC 33031–33033 (CIG 00333–335), three adult males, collected at Puerto El Balsamo, Municipality of José Azueta (17.9812, -101.2292, 1,900 m asl; datum = WGS84), Guerrero, Mexico on 5 June 2015 by Christoph I. Grünwald, Nadia Pérez-Rivera, and Héctor Franz-Chávez.

Diagnosis. Based on the phylogenetic analysis, this species is a member of the genus *Eleutherodactylus*, subgenus *Syrrhophus*, as defined by Hedges et al. (2008); and in the *Eleutherodactylus* (*Syrrhophus*) *nitidus* species series and the *Eleutherodactylus* (*Syrrhophus*) *nitidus* species group as defined by Grünwald et al. (2018) based on the condition of the tympanic annuli, ventral epidermis, and visceral peritoneum. A small frog, adult males measure 23.3–25.3 mm SVL; vocal slits are present in males; digital tips are expanded, 1.4–2.3 times the width of the narrowest part the finger on the third and fourth fingers; finger lengths are I-II-IV-III, fingers moderately long, with third finger length ranging from 13–21% of SVL; compact lumbar gland in the inguinal region present but indistinct, visible in live specimen; ventral epidermis semi-translucent and the visceral peritoneum is clear, not white, abdominal vein barely visible on the venter of live specimens against the background of the viscera; limbs moderate, TL/SVL ratio is 0.41–0.56, FeL/SVL ratio is 0.38–0.46 and TotFL/ SVL ratio is 0.61–0.74; snout short, END/ SVL ratio is 0.10–0.11; tympanum small, indistinct and round, tympanic annuli not visible in live specimen; TW/EW ratio is 0.26–0.28. The dorsal skin is smooth to slightly pustulate. Dorsal coloration is reddish-tan or brown. A pale brown or reddish interorbital bar always present, and a pale mid-dorsal blotch of the same color as the interorbital bar is present. Upper arms pale and unmarked, dark transverse bands present on forearms and legs, and inguinal flash coloration orange or yellow present on groin and sometimes on posterior portion of thighs. Ventral coloration whitish or gray with some darker gray spots or indistinct marbling. The mating call of adult males is a quick chirp (“peep,” see below; Fig. 3).

Comparisons. *Eleutherodactylus sentinelus* can be distinguished from all species in the *Eleutherodactylus* (*Syrrhophus*) *longipes* species series by: possessing a small, indistinct tympanum with no tympanic annulus visible and with a diameter less than 30% of diameter of the eye; by possessing a visceral peritoneum which is not white, so that the abdominal vein on the venter is not clearly evident against a white background in life; and by possessing a distinct, raised lumbar gland above

Table 1. Morphological measurements of *Eleutherodactylus maculabialis* sp. nov. specimens. See text for definitions of measurement acronyms.

| | CIG 916 | CIG 917 | CIG 918 | CIG 919 | CIG 920 | CIG 921 | CIG 922 | CIG 923 | CIG 940 | CIG 941 | CIG 945 | CIG 946 | CIG 947 | CIG 949 |
|----------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| SVL | 19.26 | 22.27 | 21.05 | 22.05 | 22.95 | 23.47 | 24.65 | 21.3 | 20.46 | 17.9 | 23.88 | 22.01 | 20.13 | 21.67 |
| HL | 6.86 | 7.45 | 7.3 | 7.43 | 7.57 | 7.78 | 8.07 | 7.18 | 7 | 6.51 | 7.77 | 7.2 | 6.8 | 7.27 |
| TW | 0.68 | 0.71 | 0.68 | 0.72 | 0.73 | 0.73 | 0.74 | 0.72 | 0.67 | 0.63 | 0.67 | 0.67 | 0.66 | 0.67 |
| ED | 2.38 | 2.78 | 2.57 | 2.56 | 2.6 | 2.68 | 2.75 | 2.53 | 2.44 | 2.23 | 2.73 | 2.5 | 2.41 | 2.48 |
| EIW | 1.28 | 1.37 | 1.3 | 1.4 | 1.39 | 1.51 | 1.51 | 1.25 | 1.33 | 1.2 | 1.51 | 1.43 | 1.47 | 1.46 |
| IOD | 4.12 | 4.35 | 4.38 | 4.41 | 4.66 | 4.76 | 4.73 | 4.23 | 3.82 | 3.41 | 4.18 | 4.08 | 4.12 | 4.11 |
| IND | 2.15 | 2.32 | 2.36 | 2.34 | 2.41 | 2.48 | 2.53 | 2.22 | 2.15 | 2.04 | 2.45 | 2.22 | 2.2 | 2.22 |
| END | 2.24 | 2.66 | 2.4 | 2.36 | 2.43 | 2.51 | 2.5 | 2.31 | 2.2 | 2.08 | 2.51 | 2.3 | 2.26 | 2.31 |
| ETD | 0.74 | 0.81 | 0.85 | 0.84 | 0.86 | 0.88 | 0.89 | 0.85 | 0.84 | 0.84 | 0.9 | 0.88 | 0.84 | 0.87 |
| UpL | 5.03 | 5.33 | 5.06 | 5.08 | 6 | 6.31 | 5.9 | 5.51 | 5.1 | 4.22 | 5.6 | 5.28 | 4.84 | 4.94 |
| Fol | 6.12 | 6.6 | 6.07 | 6.51 | 7.17 | 7.47 | 7.18 | 6.52 | 6.15 | 5.24 | 6.9 | 6.15 | 5.86 | 5.9 |
| HaL | 4.72 | 5.55 | 5.07 | 5.22 | 5.3 | 5.5 | 5.46 | 5 | 4.53 | 4.05 | 5.54 | 4.95 | 5.06 | 5.12 |
| F3PW/F3W | 1.8 | 1.6 | 2 | 2.1 | 1.7 | 1.9 | 1.8 | 1.7 | 1.6 | 1.4 | 1.6 | 1.4 | 1.8 | 1.5 |
| F4PW/F4W | 1.9 | 1.7 | 2 | 2.1 | 1.6 | 1.9 | 1.9 | 1.6 | 1.8 | 1.5 | 1.6 | 1.5 | 1.8 | 1.4 |
| FeL | 9.05 | 10.06 | 9.65 | 9.66 | 10.03 | 10.49 | 10.44 | 8.75 | 8.6 | 8.22 | 9.92 | 9.78 | 9.04 | 9.09 |
| TL | 9.75 | 10.46 | 10.23 | 10.18 | 11 | 11.5 | 10.97 | 9.9 | 9.4 | 8.6 | 10.89 | 10.17 | 9.95 | 9.75 |
| TotFL | 14.08 | 15.75 | 15.13 | 15.43 | 15.81 | 16.12 | 16.4 | 14.53 | 13.4 | 12.42 | 15.83 | 14.6 | 14.57 | 13.93 |
| ITP | 0.56 | 0.6 | 0.57 | 0.55 | 0.68 | 0.67 | 0.69 | 0.58 | 0.49 | 0.39 | 0.51 | 0.58 | 0.47 | 0.4 |
| MPT | 0.78 | 0.9 | 0.79 | 0.84 | 0.92 | 0.96 | 0.95 | 0.77 | 0.75 | 0.69 | 0.73 | 0.73 | 0.7 | 0.7 |
| OPT | 0.28 | 0.45 | 0.4 | 0.37 | 0.46 | 0.43 | 0.44 | 0.37 | 0.3 | 0.25 | 0.34 | 0.35 | 0.35 | 0.32 |
| IMTL | 0.79 | 0.83 | 0.76 | 0.73 | 0.79 | 0.91 | 0.95 | 0.68 | 0.67 | 0.64 | 0.8 | 0.78 | 0.74 | 0.72 |
| OMTL | 0.44 | 0.55 | 0.45 | 0.45 | 0.56 | 0.6 | 0.63 | 0.37 | 0.32 | 0.4 | 0.45 | 0.43 | 0.41 | 0.45 |
| TW/ED | 0.29 | 0.26 | 0.26 | 0.28 | 0.28 | 0.27 | 0.27 | 0.28 | 0.27 | 0.28 | 0.25 | 0.27 | 0.27 | 0.27 |

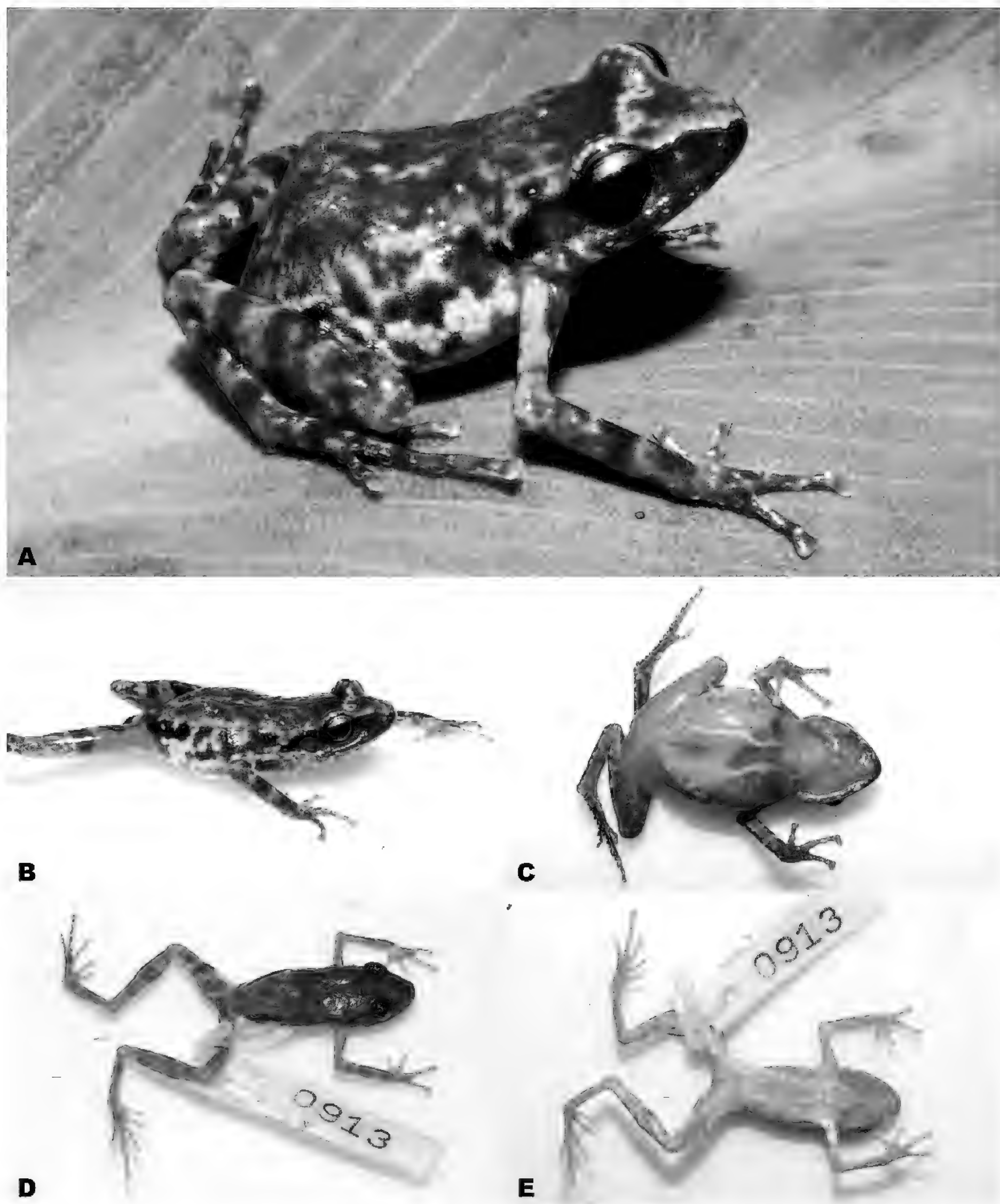


Fig. 4. Holotype of *Eleutherodactylus sentinelus* sp. nov., MZFC 33306 (CIG 00913) from 8.9 km SW of Puerto El Balsamo, Municipality of José Azueta, Guerrero, Mexico. **(A)** Dorsolateral perspective in life. **(B)** Lateral perspective in life. **(C)** Ventral perspective in life. **(D)** Dorsal perspective in preservative. **(E)** Ventral perspective in preservative.

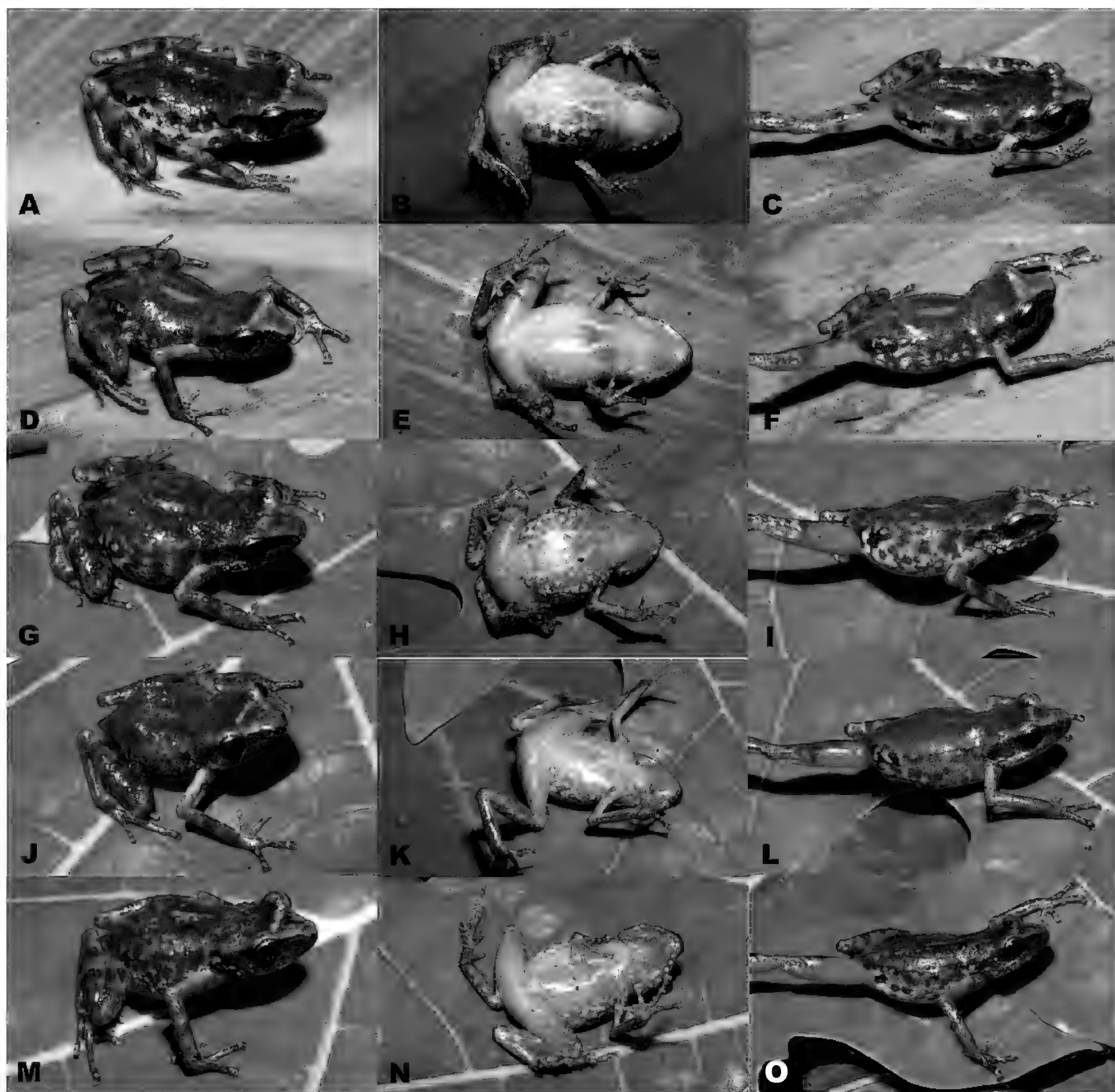


Fig. 5. Some of the paratypes of *Eleutherodactylus sentinelus* sp. nov. in life. (A–C) MZFC 33305 (CIG 00910); (D–F) MZFC 33304 (CIG 00909); (G–I) MZFC 33032 (CIG 00334); (J–L) MZFC 33031 (CIG 00333); (M–O) MZFC 33033 (CIG 00335) from Puerto El Balsamo, Municipality of José Azueta, Guerrero, Mexico.

the inguinal region.

Eleutherodactylus sentinelus can be distinguished from species of the *Eleutherodactylus* (*Syrrhophus*) *modestus* species group by the combination of possessing a compact, protruding lumbar gland above the inguinal region, digital tips which are expanded more than 1.4 times the width of the narrowest part the finger on the third and fourth fingers, and the presence of an interorbital bar.

Within its own species group, *E. sentinelus* can be distinguished from most species by possessing a compact inguinal gland which is indistinct but visible in live specimens. This differs from *E. pipilans*, *E. erythrochomus*, and *E. nebulosus*, which lack a distinct visible inguinal gland altogether. All other known species in the *E. (Syrrhophus) nitidus* species group have readily visible compact lumbar glands above the inguinal region. *Eleutherodactylus sentinelus* can be further distinguished from *E. pipilans*, *E. erythrochomus*, and *E. nebulosus* by the presence of distinct pale interorbital bar and pale-yellow inguinal flash coloration. It may be distinguished from *E. nitidus*, *E. petersi*, and *E. orarius* by the combination of smoother skin, longer limbs, and tips of digits which are expanded more than 1.4 times the narrowest part of the finger on the third and fourth fingers. It further differs from these three species by call, which is a short chirp rather than a whistle. It is distinguished from *E. albolabris* by the following characters (characters of *E. albolabris* in parentheses): lip dark, never white, with some flecking (lip white, immaculate), inguinal flash coloration always yellow (always fiery orange), ventral coloration translucent and white, with some black markings (ventral coloration completely white with bold black markings), tympanum small with TW/ED 0.25–0.28 (tympanum slightly larger with TW/ED 0.27–0.32). *Eleutherodactylus sentinelus* may be distinguished from *E. maurus* by the following (characters of *E. maurus* in parentheses): by the presence of pale interorbital bar same color as snout (*E. maurus* presents no pale interorbital bar), smooth dorsal and ventral skin (rugose or slightly rugose dorsal and ventral skin), bright yellow or orange flash colors on thighs (flash colors absent, or barely discernible), pale interorbital stripe distinct between darker head coloration (pale interorbital stripe absent or same color as dorsal surface of snout). *Eleutherodactylus sentinelus* may be distinguished from *E. syristes* and *E. maculabialis* by its mating call, which is a rapid chirp (“peep”) as opposed to a trill. *Eleutherodactylus sentinelus* can be further distinguished from the closely related *E. syristes* by having more expanded finger tips, 1.4–2.3 times the narrowest part of the digit on fingers three and four, and usually more than 1.6 (vs. 1.1–1.5 times the narrowest part of the digit on fingers three and four), and by having yellow or yellowish-orange flash colors (vs. orange or reddish flash colors). *Eleutherodactylus sentinelus* is most similar to *E.*

dilatus, from which it may be distinguished by the by much smoother skin on both the dorsum and venter (*E. dilatus* has rugose dorsal skin and pustulate venter), smaller, less distinct inguinal glands (*E. dilatus* has large, distinct inguinal glands), and a paler dorsal ground coloration (*E. dilatus* is dark brown).

Description of the holotype. Small frog (24.1 mm SVL); male; head slightly longer (7.1 mm) than wide (6.4 mm), head slightly wider than body; snout subovoid from a dorsal view and rounded from a lateral profile; tympanum indistinct, rounded with no supra-tympanic fold present; tympanum small, circular, greatest width of tympanum 0.8 mm; greatest diameter of eye 2.9 mm; tympanum width to eye diameter ratio 0.28; eyelid width 1.6 mm, a third of the IOD; first finger shorter than second finger; finger lengths from shortest to longest I-II-IV-III; digital pads on fingers two, three, and four slightly expanded, 1.6 times the narrowest point of the digit on second finger and 2.3 times the narrowest point of the digit on fingers three and four; expanded finger pads truncate; three palmar tubercles; inner palmar tubercle about 75% as large as middle palmar tubercle, outer palmar tubercle about half the size of middle palmar tubercle (Fig. 6B); toe lengths from shortest to longest I-II-V-III-IV; outer metatarsal conical with a round base, small, approximately 50% of inner metatarsal tubercle; inner metatarsal tubercle spherical shape with oval base, large, approximately 0.9 mm in length; dorsal skin smooth, lateral skin slightly shagreened, ventral skin smooth. Vocal slits present.

In life, the holotype had a dark reddish-brown dorsal ground coloration, with pale reddish interorbital bar, mid-dorsal blotch, and upper arm coloration, with the upper arm the palest. Lateral portions of the head were dark brown coloration, with small white flecks on the labial and loreal regions. Lateral coloration was brown and white. Legs and arms were ochre with dark brown transverse bars. Yellow flash colors present on the groin. Ventral coloration flesh colored with white spots and black melanophores. See Fig. 4A–C for photographs of the holotype in life.

Coloration in preservative is brown dorsum, with some paler brown areas on the lower parts of the back. Indistinct cream-colored interorbital bar, upper arms and groin pale tan. Inguinal gland black. White marbling on lateral surfaces. Legs and arms pale tan with darker brown transverse bands. Ventral surfaces white, unmarked, throat yellowish (Fig. 4D–E).

Measurements of the holotype (in mm). IND 2.4, IOD 4.8, END 2.5, ETD 1.1, UpL 6.2, FoL 7.9, HaL 6.3, F1L 2.3, F1PW 0.5, F1W 0.3, F2L 2.7, F2PW 0.6, F2W 0.4, F3L 4.0, F3PW 1.0, F3W 0.4, F4L 3.1, F4PW 1.0, F4W 0.4, IPTL 0.6, MPTL 0.9, OPTL 0.4, FeL 11.3, TL 12.3, TaL 7.2; FL 10.9, T2L 3.1, T2PW 0.7, T2W 0.4, T3L 4.9, T3PW 0.7, T3W 0.4, T4L 7.9, T4PW 0.8, T4W 0.4,

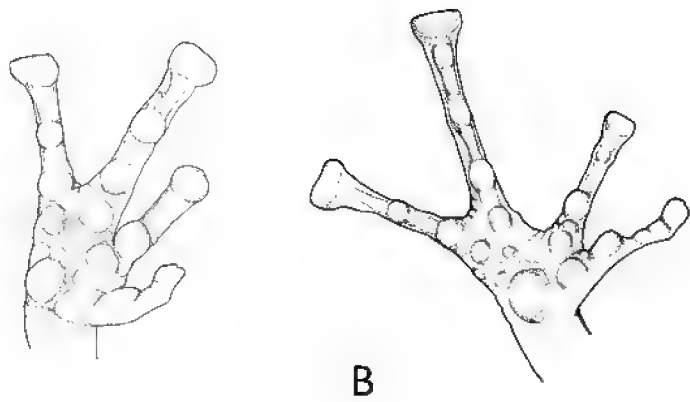


Fig. 6. (A) Ventral aspect of hand of holotype of *Eleutherodactylus maculabialis* sp. nov., MZFC 33312 (CIG 00921) from 11.4 km S of Puerto de Gallo, Municipio de Atoyac de Álvarez, Guerrero, Mexico. (B) Ventral aspect of hand of holotype of *Eleutherodactylus sentinelus* sp. nov., MZFC 33306 (CIG 00913) from 8.9 km SW of Puerto El Balsamo, Municipality of José Azueta, Guerrero, Mexico.

T5L 3.5, T5PW 0.5, T5W 0.4, IMTL 1.0, OMTL 0.6, FeL/SVL 46%, TL/SVL 50%, Ha/SVL 25%, FL/SVL 44%, HL/SVL 33%, HW/SVL 29%.

Variation. SVL from 23.3–25.3 mm (24.2 ± 0.81). Expanded finger pads on third and fourth fingers vary from 1.4–2.3 times the narrowest part of the digit, with average 1.85 ± 0.26 on the third finger and average 1.78 ± 0.36 on the fourth finger. Dorsal ground coloration ranges across different shades of reddish brown (MZFC 33304), tan (MZFC 33031, 33306), and brown (MZFC 33032–3, 33304–5). Venter typically gray, with white and black markings, although these markings range from sparse to almost complete reticulation. Morphological variation is presented in Table 2.

Distribution and ecology. This species is known only from the vicinity of the type locality in the western-most extension of the Sierra Madre del Sur of Guerrero (Fig. 7A). It has been collected at elevations ranging from 1,300–1,900 m asl, on steep mountain sides in humid pine-oak forest, oak woodland and pine-oak woodland, and tropical deciduous forest ecotone. At the type locality, this species is sympatric with *E. petersi*. All individuals of *E. sentinelus* have been observed after the onset of the rainy season in the months of June and July. Individuals were found calling on small bushes or rocks. All were found active at night.

Etymology. This species is named after latin *sentinel*, meaning guard or outpost, in reference to its type locality, a mountain which stands out from the north and west as the first outpost of the Sierra Madre del Sur of Guerrero.

Summary Data for *Eleutherodactylus nitidus* Species Group Members

To help differentiate between the two new species

described above, and the related species in the *Eleutherodactylus nitidus* species group, important morphological, mensural, and call differences of all of the species in this group are collated into a single table (Table 3), and photographs of related species in the *E. nitidus* species group are provided (Figs. 9–10). The distributions of the species in the *E. nitidus* group are mapped in Figs. 7 and 13.

Differentiating the Advertisement Calls of Closely Related *Eleutherodactylus nitidus* Species Group Members

Recordings were made from 120 calling males of all 24 species of *Eleutherodactylus* from western Mexico. The calls of the species analyzed were found to fall into five different categories of a rapid burst whistle (trill), a drawn-out whistle (whistle), a strong high-pitched chirp (peep), a soft high-pitched chirp (chirp), and a drawn-out chirp (pipe). Of the species analyzed herein, four (*E. dilatatus*, *E. nebulosus*, *E. pipilans*, *E. sentinelus*) produce a strongly high-pitched chirp (peep), four (*E. albolabris*, *E. nitidus*, *E. orarius*,

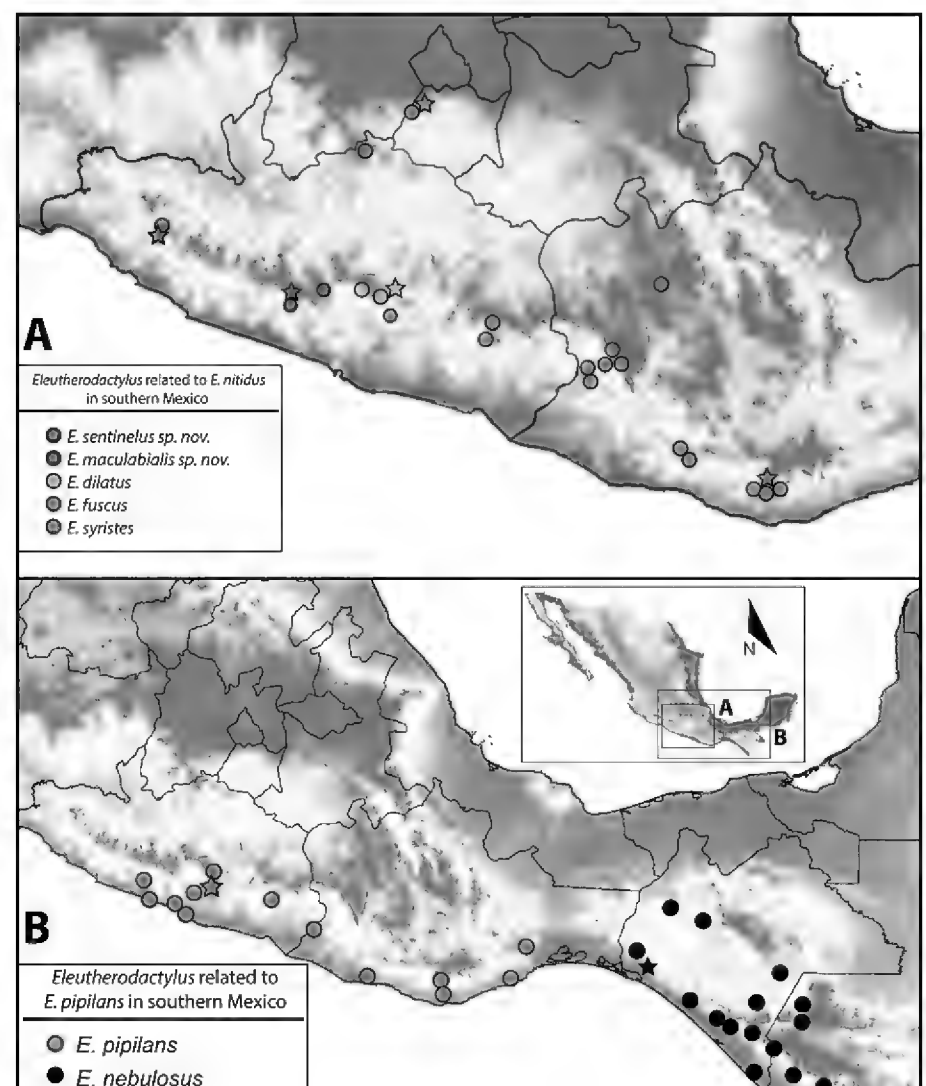


Fig. 7. (A) Map showing the type localities and distribution of *Eleutherodactylus* species related to *E. nitidus* in southern Mexico. The stars represent type localities and circles represent additional localities, with each color coded for the species: *E. sentinelus* sp. nov. (purple), *E. maculabialis* sp. nov. (green), *E. dilatatus* (pink), *E. maurus* (yellow), and *E. syristes* (blue). (B) Map showing the type localities and distribution of *Eleutherodactylus* species related to *E. pipilans* in southern Mexico. The red star represents the type locality of *E. pipilans* and red circles represent additional localities. The black star represents the type locality of *E. nebulosus* and black circles represent additional localities.



Fig. 8. (A) Type locality of *Eleutherodactylus maculabialis* sp. nov. at 11.4 km S of Puerto de Gallo, Municipio de Atoyac de Álvarez, Guerrero, Mexico. (B) Type locality of *Eleutherodactylus sentinelus* sp. nov. at 8.9 km SW of Puerto El Balsamo, Municipality of José Azueta, Guerrero, Mexico.

E. petersi) produce a drawn-out whistle (whistle), two (*E. maculabialis* and *E. syristes*) produce multi-note or pulsed calls (trill) of various rates and notes, and one (*E. maurus*) produces a slow and drawn-out chirp (pipe). While a detailed account is given of the calls of the species we describe here, as well as some of their relatives, we refrain from giving detailed descriptions of the calls of *E. nitidus*, *E. albolabris*, *E. orarius*, *E. petersi*, *E. pipilans*, *E. nebulosus*, and “*E. rubrimactulatus*” pending a more detailed taxonomic study of this species complex.

***Eleutherodactylus dilatus*.** The advertisement call of *E. dilatus* is a single high-pitched “chirp” best described as a “peep” (Fig. 11C). Calls recorded at the type locality consist of a rapid chirp, with an average duration of 110 ms, and a dominant frequency ranging between starting at 2,550 kHz and 2,780 kHz.

***Eleutherodactylus maculabialis*.** The advertisement call of *E. maculabialis* is a relatively slow multi-note “trill” (Fig. 3). Calls recorded at the type locality consist of slow six-note trills with a duration of 180–210 ms, and a dominant frequency starting at 2,600–2,900 kHz and rising to 3,050–3,200 kHz. The call interval is about 40–55 ms (Fig. 3A). At a nearby

locality at 1,320 m asl (Fig. 3B), calls were recorded of two males which varied from the type locality in consisting of five-note trills with an average duration of 230 ms and a dominant frequency starting at 3,630 kHz and reaching 4,000 kHz (Table 4).

***Eleutherodactylus maurus*.** The advertisement call of *E. maurus* is a single, drawn-out “chirp” best described as a “pipe.” Calls recorded near Ocuilan, in Estado de México, consisted of a single chirp with a duration of 205 ms, and a dominant frequency starting at 2,760 kHz and rising to 3,150 kHz. The amplitude was strongest at the middle of a call (Fig. 11D). At a locality near Taxco, Guerrero, a call of *E. maurus* was recorded which consisted of a single, drawn-out chirp. However, the call was longer, averaging 275 ms and the amplitude was distributed in three sub-pulses. This indicates a further need to investigate this population.

***Eleutherodactylus sentinelus*.** The advertisement call of *E. sentinelus* is a single high-pitched “chirp” best described as a “peep” (Fig. 3). Calls recorded at the type locality consist of a rapid chirp, with an average duration of 160 ms, and a dominant frequency starting at 2,560 kHz and rising to 3,100 kHz (Fig. 3D). Calls recorded above the type locality at 1,900 m asl (Fig. 3C) are slightly shorter and of higher frequency, with an average duration of 120 ms, and a dominant frequency starting at 2,700 kHz and finishing at 3,300 kHz (Table 4).

***Eleutherodactylus syristes*.** The advertisement call of *E. syristes* is a rapid but long multiple-pulse “trill” (Fig. 11A–B). Calls recorded at two different localities in Guerrero consisted of 49–60 pulses, about 10 ms apart, with a total duration of the call averaging 500–560 ms. The dominant frequency at Agua de Obispo, Guerrero, was between 2,700–3,170 kHz, starting lower, peaking, and then lowering again (Fig. 11A). At a second locality, slightly lower than Agua de Obispo, east of Highway 95, the calls tended to have a dominant frequency ranging between 3,000–3,390 kHz (Fig. 11B).

***Eleutherodactylus albolabris*.** The advertisement call of *E. albolabris* is a single, multi-pulsed whistle, with the call continuous amongst the pulses and with a duration of approximately 150–250 ms (Fig. 11F). Calls recorded at the type locality at Agua de Obispo had a duration of 160 ms, and started at a dominant frequency of 2,840 kHz rising to 3,015 kHz. Calls varied between 7–10 continuous pulses. At a second locality, near Vallecitos in the Municipality of José Azueta, Guerrero, the calls had a duration of 240 ms, and started at a dominant frequency of 2,740 kHz which rose to 2,915 kHz. Calls started with a multi-pulsed trill and then ended with several distinct pulses. This population’s call is best described as a combination of a “trill” with a “whistle” (Fig. 11E).

Table 2. Morphological measurements of *Eleutherodactylus sentinelus* sp. nov. specimens. See text for definitions of measurement acronyms.

| | CIG-333 | CIG-334 | CIG-335 | CIG-907 | CIG-908 | CIG-909 | CIG-910 | CIG-913 |
|----------|---------|---------|---------|---------|---------|---------|---------|---------|
| SVL | 24.37 | 24.48 | 25.30 | 25.1 | 23.31 | 23.41 | 23.25 | 24.54 |
| HL | 8.58 | 8.70 | 8.67 | 7.88 | 7.1 | 7.15 | 7.1 | 8.03 |
| TW | 0.74 | 0.76 | 0.80 | 0.76 | 0.74 | 0.74 | 0.74 | 0.81 |
| ED | 2.63 | 2.68 | 2.77 | 2.67 | 2.77 | 2.8 | 2.73 | 2.85 |
| EIW | 1.55 | 1.54 | 1.6 | 1.58 | 1.53 | 1.54 | 1.54 | 1.6 |
| IOD | 4.80 | 4.83 | 4.87 | 4.73 | 4.54 | 4.5 | 4.5 | 4.8 |
| IND | 2.58 | 2.37 | 2.55 | 2.34 | 2.31 | 2.33 | 2.28 | 2.44 |
| END | 2.80 | 2.74 | 2.78 | 2.59 | 2.4 | 2.41 | 2.38 | 2.52 |
| ETD | 1.03 | 1.00 | 1.01 | 1.03 | 0.97 | 0.95 | 0.96 | 1.07 |
| UpL | 5.76 | 6.26 | 6.40 | 4.52 | 5.32 | 5.4 | 5.37 | 6.2 |
| FoL | 6.74 | 7.43 | 7.56 | 7.15 | 6.8 | 6.93 | 6.87 | 7.92 |
| HaL | 5.5 | 5.4 | 6.2 | 5.25 | 5.11 | 5 | 5.05 | 6.25 |
| F3PW/F3W | 1.70 | 1.80 | 1.80 | 2.2 | 1.7 | 1.7 | 1.6 | 2.3 |
| F4PW/F4W | 1.60 | 1.90 | 1.70 | 2.3 | 1.4 | 1.5 | 1.5 | 2.3 |
| FeL | 10.26 | 10.58 | 11.00 | 9.62 | 9.35 | 9.26 | 9.3 | 11.28 |
| TL | 11.03 | 11.65 | 11.33 | 10.31 | 9.95 | 10.12 | 9.9 | 12.33 |
| TotFL | 16.4 | 16.3 | 17.5 | 15.4 | 15.51 | 15.35 | 15.4 | 18.05 |
| IPT | 0.58 | 0.70 | 0.74 | 0.5 | 0.58 | 0.6 | 0.59 | 0.65 |
| MPT | 0.84 | 1.00 | 1.07 | 0.77 | 0.88 | 0.86 | 0.87 | 0.86 |
| OPT | 0.4 | 0.45 | 0.45 | 0.32 | 0.39 | 0.42 | 0.42 | 0.4 |
| IMTL | 0.50 | 0.58 | 0.46 | 0.52 | 0.47 | 0.46 | 0.47 | 0.64 |
| OMTL | 0.90 | 0.92 | 1.04 | 0.74 | 0.84 | 0.85 | 0.83 | 0.99 |
| TW/ED | 0.28 | 0.28 | 0.29 | 0.28 | 0.27 | 0.26 | 0.27 | 0.28 |

Molecular Analysis of the *Eleutherodactylus nitidus* Species Group

The molecular phylogeny based on the mitochondrial rRNA 16S recovered a well-supported *Eleutherodactylus nitidus* species group (posterior probability (pp) 1; Figs. 12 and S1), which is sister to the *E. modestus* group as defined by Grünwald et al. (2018). As with previous phylogenies of the group based on 16S, some of the intermediate nodes in the phylogeny are not well supported (pp < 0.5), and we have collapsed all nodes below this value.

In the *Eleutherodactylus nitidus* species group, we recovered two main clades. The first one is composed of *E. pipilans*, *E. erythrochomus*, and *E. nebulosus*, while the second group includes all the other species. In the second group, many of the intermediate nodes have little to no support. However, individual species do show strong support (pp = 1) in most cases, including *E. dilatus*, *E. sentinelus*, *E. maurus*, and *E. syristes*, while *E. maculabialis* has a posterior support of 0.86.

All the remaining species in the group form a second, well-supported clade (pp = 0.99). In this clade, we recovered an early split between

Eleutherodactylus albolabris and the other species, which include *E. orarius*, *E. petersi*, *E. nitidus*, and a hitherto undescribed form from Jalisco and Nayarit (Fig. 13). We refrain from describing the western-most form at this time, as material from the type locality of *E. petersi* is unavailable, so the relationship of the western form with *E. petersi* remains unclear.

We believe that a more detailed study of the taxa related to *E. nitidus* is needed, when more thorough sampling is available and employing more population-level specific tools, such as genome-wide SNP data, in order to better understand the patterns of gene-flow and introgression.

Discussion

With the descriptions of the two species here, the number of taxa in the subgenus *Syrrhophus* increases to 37, with 35 in continental North America and two in Cuba. Guerrero is one of the most speciose states, with nine recognized species and several undescribed taxa awaiting description (Grünwald, pers. obs.). All members of the subgenus *Syrrhophus* recorded from Guerrero thus far belong to the *Eleutherodactylus nitidus* species group as defined by Grünwald et

Table 3. Key comparative characters of members of the *Eleutherodactylus nitidus* species group.

| | <i>E. albolabris</i> | <i>E. dilatus</i> | <i>E. erythrochomus</i> | <i>E. maculabilais</i> sp. nov. | <i>E. maurus</i> | <i>E. nebulosus</i> | <i>E. nitidus</i> | <i>E. orarius</i> | <i>E. petersi</i> | <i>E. pipilans</i> | <i>E. sentinelus</i> sp. nov. | <i>E. syristes</i> |
|-------------------------------|------------------------|---------------------------|-------------------------|------------------------------------|---------------------------|----------------------|--------------------------|--------------------------|--------------------------|--------------------|----------------------------------|---|
| Size | Medium | Medium | Large | Small | Small | Medium | Medium | Medium | Medium | Large | Medium | Small |
| SVLadult males (range) | 23.0–26.8 | 23.8–25.7 | 24.9–30.0 | 17.9–24.7 | 20.7–24.3 | 22.9–28.3 | 24.3–26.3 | 24.6–28.0 | 23.9–26.3 | 25.5–29.6 | 23.3–25.3 | 21.7–24.6 |
| Condition of interorbital bar | Indistinct, pale | Present, pale | Absent | Present, pale | Present, pale | Absent | Indistinct, pale | Indistinct, pale | Indistinct, pale | Absent | Present, pale | Present, pale |
| Pale mid-dorsal blotch | Sometimes present | Absent | Absent | Absent | Absent | Absent | Present | Sometimes present | Present | Absent | Present | Absent |
| Coloration of lip | White | Dark with pale flecking | As head | Dark with pale spots | Dark with pale flecking | Dark with pale spots | Mottled | White, mottled with dark | Mottled | As head | Dark with pale flecking | Dark, variously spotted |
| Inguinal flash coloration | Orange | Yellow | Absent | Varied, yellow / orange | Yellow | Absent | Faint, yellow-orange | Faint, yellow-orange | Faint, yellow-orange | Absent | Yellow | Varied, yellow / orange |
| Ventral coloration | White with black spots | Gray with white and black | Transparent | Gray with white and black | Gray with white and black | Transparent | White with dark mottling | White with dark mottling | White with dark mottling | Transparent | Transparent with white and black | Transparent and white, with black spots |
| Dorsal skin texture | Smooth | Not smooth | Smooth | Smooth | Not smooth | Smooth | Not smooth | Not smooth | Not smooth | Smooth | Smooth | Smooth |
| Ventral skin texture | Slightly rugose | Rugose | Smooth | Smooth | Rugose | Smooth | Slightly rugose | Slightly rugose | Slightly rugose | Smooth | Smooth | Smooth |
| Condition of inguinal gland | Very distinct | Very distinct | Indistinct | Distinct | Very distinct | Indistinct | Very distinct | Very distinct | Very distinct | Indistinct | Very distinct | Distinct |
| 3FPW/3FW | 1.3–1.9 | 1.5–1.7 | 2.3–3.8 | 1.4–2.1 | 1.3–1.6 | 1.1–1.5 | 1.1–1.5 | 1.2–1.4 | 1.1–1.7 | 1.5–1.9 | 1.7–2.3 | 1.1–1.9 |
| 4FPW/4FW | 1.3–1.9 | 1.5–1.8 | — | 1.4–2.1 | 1.3–1.7 | 1.1–1.5 | 1.1–1.5 | 1.2–1.4 | 1.1–1.7 | 1.5–2.0 | 1.5–2.3 | 1.2–1.8 |
| TW/ED | 0.27–0.32 | 0.25–0.35 | 0.33–0.51 | 0.25–0.28 | 0.28–0.31 | 0.35–0.38 | 0.25–0.29 | 0.25–0.29 | 0.25–0.29 | 0.30–0.36 | 0.26–0.28 | 0.25–0.29 |
| Call | Whistle | Peep | Peep | Trill | Pipe | Peep | Whistle | Whistle | Whistle | Peep | Peep | Trill |

Table 4. Advertisement call data of *Eleutherodactylus maculabialis* sp. nov. and *Eleutherodactylus sentinelus* sp. nov.

| | <i>E. maculabialis</i> | <i>E. sentinelus</i> |
|-----------------------------------|------------------------|----------------------|
| Call type | Trill | Peep |
| Dominant frequency (kHz) | 3.28 ± 532.5 | 2.91 ± 85.0 |
| Call length (ms) | 212.5 ± 20.55 | 140 ± 20.0 |
| Call rate (m⁻¹) | 5.49 ± 1.1 | 2.84 ± 0.19 |
| Call rise time (ms) | 18.5 ± 2.25 | 13 ± 4.0 |
| Pulse rate | 5.5 ± 0.25 | 1 ± 0 |
| Call interval | 19.87 ± 4.28 | 36.94 ± 10.52 |

al. (2018). Based on our phylogenetic analysis, *E. dilatus*, *E. maurus*, and *E. syristes* are closely related and restricted to high-elevation moist mountainous areas. The new taxa described herein are closely related to these species, with *E. maculabialis* being a sister taxon to *E. syristes* and *E. sentinelus* being a sister taxon to *E. dilatus*. They collectively have an allopatric distribution which covers most of Guerrero's high mountains.

Based on collection locality information, *E. maculabialis* has a known distribution of approximately 150 km² in the Sierra Madre del Sur. Widespread on the windward slopes of the great Cerro Teotepec, it has been collected at several localities along the road that ascends it, and also at some localities in the central Sierra Madre del Sur north of the Cerro Teotepec (e.g., La Guitarra, Yerba Santa). It appears to be isolated from the nearest locality of its closest relative, *E. syristes* (Agua de Obispo), by the combination of the dry and tropical Rio Papagayo Valley and the cooler pine forests of Omiltemi area which is inhabited by *E. dilatus*. *Eleutherodactylus maculabialis* seems to be separated from *E. dilatus* primarily by habitat, with the former inhabiting humid pine-oak forest, cloud forest, and tropical wet forest-oak woodland ecotone, whereas the latter is restricted to slightly drier pine forest and pine-oak woodland. A specimen (MZFC 12930) which appears to be *E. maculabialis*, was collected at the western extreme of the Omiltemi State Park. Unfortunately, it is not well preserved, and the absence of molecular data makes it impossible to definitively assign this specimen to this species. However, if this population is indeed *E. maculabialis*, it would suggest a much larger range for this species and closer proximity to the range of *E. dilatus*.

The limited number of known collecting localities for *E. sentinelus* suggest that it has the smallest range of the *E. nitidus* species group, seconded by its close relative, *E. dilatus*. As currently understood, the distribution of *E. sentinelus* is approximately 22 km², while *E. dilatus* has a known distribution of approximately 76 km². These two species appear to be separated by around 160 km of Sierra Madre del Sur where neither has been collected, and only the lower elevation species of *E. nitidus*, *E. petersi*, *E. albolabris*, and *E. maculabialis* have been collected. More sampling is needed to determine the relationship of the distributions of *E. sentinelus* and

E. maculabialis in the western portions of the Sierra Madre del Sur.

Eleutherodactylus maculabialis is a species that seems to be abundant where it occurs. While exact man-hours per specimen collected were not logged while collecting this species, numerous specimens were collected with each attempt to locate the species, and many more were heard calling. *Eleutherodactylus sentinelus* seems to be less abundant than its congeners. During four attempts to collect specimens during the breeding season (June and July), no specimens were heard or collected during one of them, only three specimens were heard during another, and the remaining two attempts resulted in more than a dozen specimens heard and collection of the type series. This contrasts with our experiences with closely related *E. dilatus*, *E. maculabialis*, and *E. syristes*, of which dozens of specimens were heard calling at all localities during all attempts to collect these species.

From a conservation perspective, *E. maculabialis* does not appear to have any major threats at this time. Small-scale agriculture is present at some locations throughout its range, but does not seem to largely impact this species, and the species continues to be present in disturbed plots. However, both illegal logging activity and illegal poppy farming were previously rampant on the lower slopes of Cerro Teotepec. In addition to destroying the forest being logged directly, the illegal logging also causes heavy siltation and landslides which destroy large swaths of the surrounding vegetation. The illegal poppy plantations also caused large swaths of suitable habitat to be completely cleared. We propose this species to be provisionally classified as Endangered B1ab(iii), based on IUCN Red List criteria that the range is more than 100 km² but smaller than 5,000 km², it occurs in only a couple of threat-defined locations, and there is ongoing decline in the extent and quality of its habitat due to small-scale agriculture, cattle ranching, illegal logging, opium poppy farming, road construction, and the resulting siltation due to these activities.

Habitat transformation due to small-scale agriculture is widely present within the distribution range of *E. sentinelus*, which seems to be limited to approximately 22 km². While these frogs seem to persist in disturbed areas, they are much less abundant than congeners in similar areas (Grünwald, pers. obs., see above). Due to the relative rarity of these frogs combined with the small known distribution, we

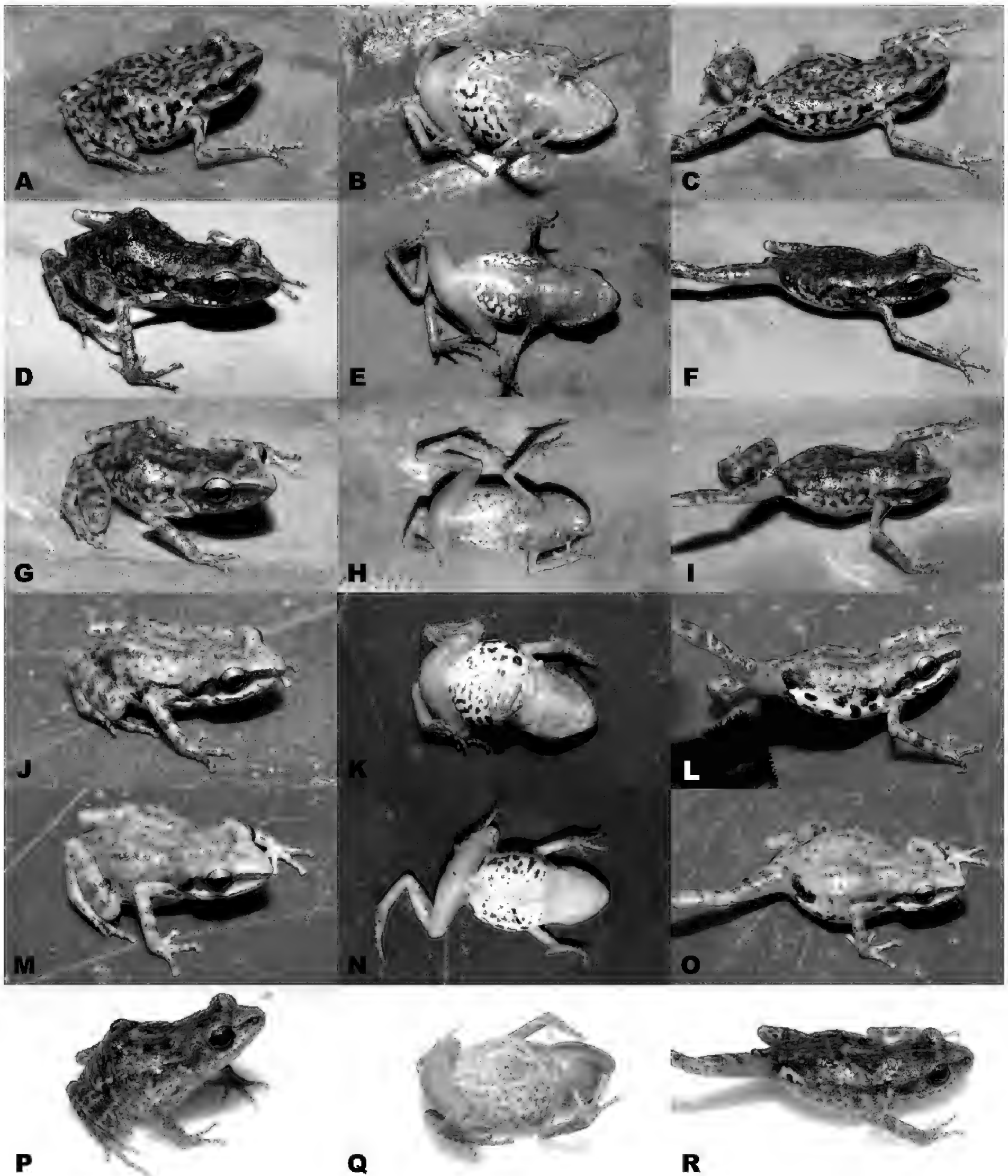


Fig. 9. Comparison photos of *Eleutherodactylus* species related to *E. nitidus* in life. (A–I) *E. syristes* from the vicinity of Agua de Obispo, Municipality of Chilpancingo, Guerrero, Mexico. (J–O) *E. albolabris* from Agua de Obispo, Municipality of Chilpancingo, Guerrero, Mexico. (P–R) *E. nitidus* from Yerba Santa, Municipality of General Heliodoro Castillo, Guerrero, Mexico.

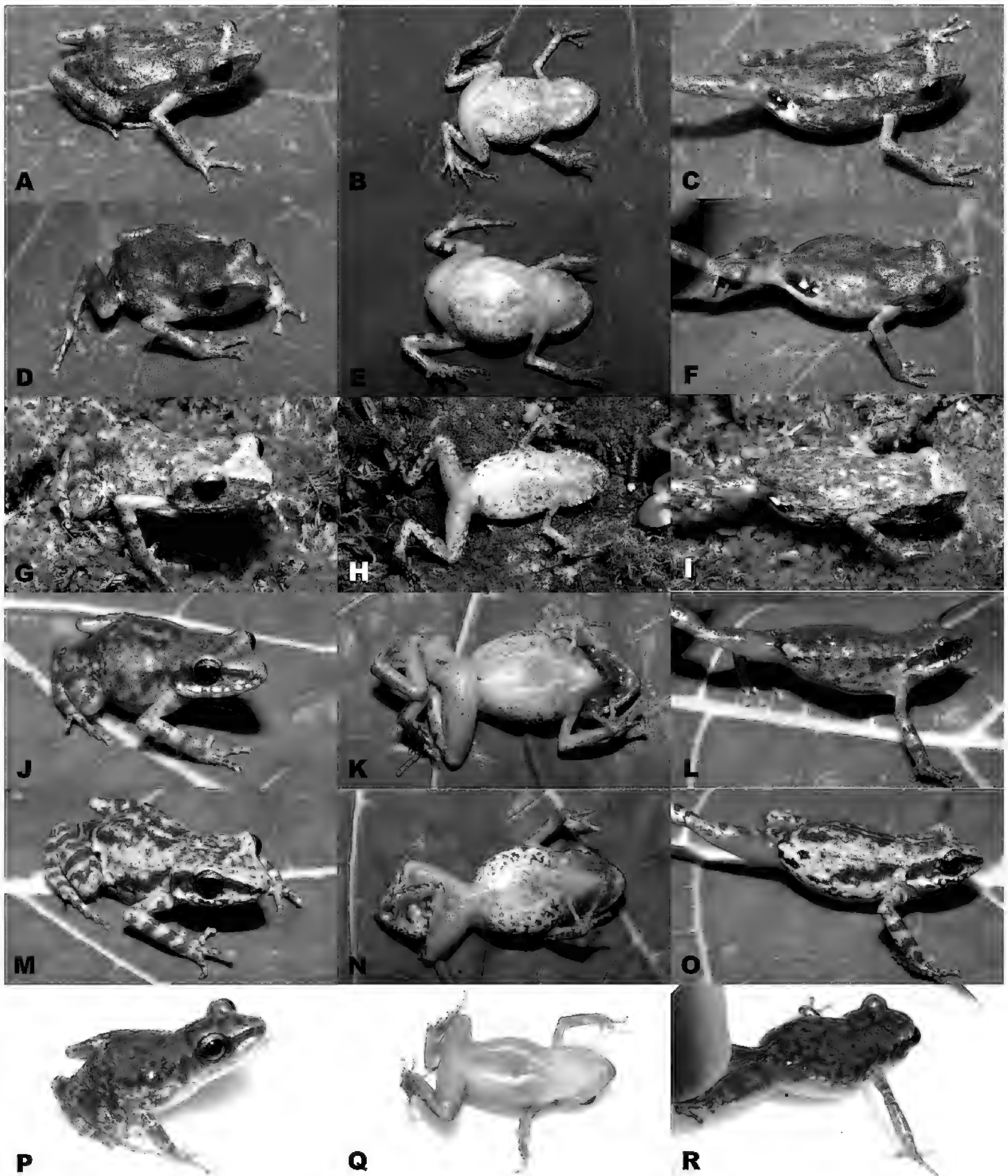


Fig. 10. Comparison photos of *Eleutherodactylus* species related to *E. nitidus* in life. (A–I) *E. dilatatus* from Omiltemi, Municipality of Chilpancingo, Guerrero, Mexico. (J–O) *E. petersi* from Puerto El Balsamo, Municipality of José Azueta, Guerrero, Mexico. (P–R) *E. pipilans* from Acahuizotla, Municipality of Chilpancingo, Guerrero, Mexico.

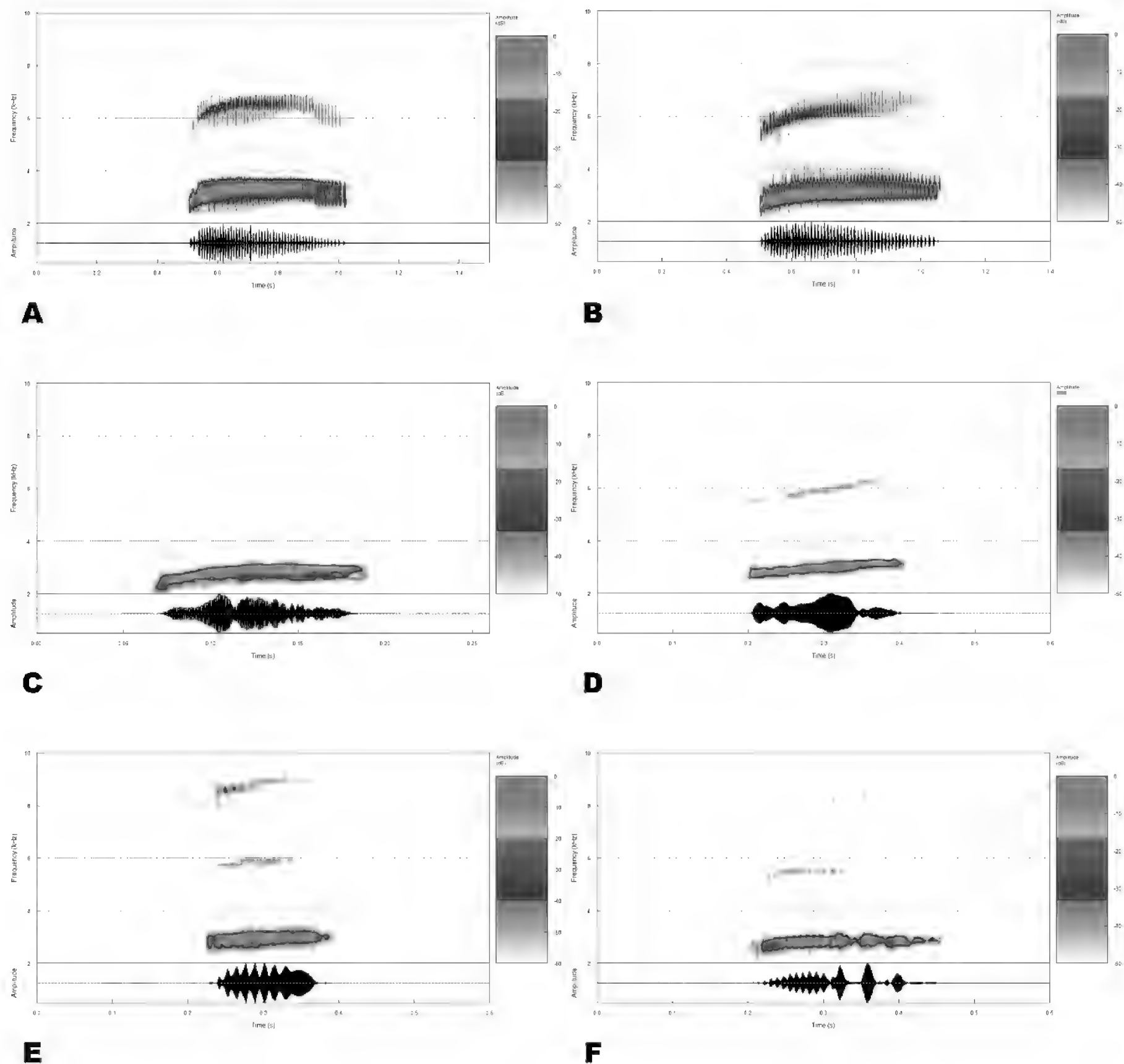


Fig. 11. Oscillograms and spectrograms of the advertisement calls of adult males of *Eleutherodactylus* species related to *E. maculabialis* sp. nov. and *E. sentinelus* sp. nov. (A) *E. syristes* from Agua del Obispo, Guerrero, Mexico. (B) *E. syristes* from east of Hwy. 95, near Acahizotla, Guerrero, Mexico. (C) *E. dilatus* from Municipality of Chilpancingo, Guerrero, Mexico. (D) *E. maurus* from Municipality of Ocuilán, Estado de México, Mexico. (E) *E. albolabris* from Municipality of Agua de Obispo, Guerrero, Mexico. (F) *E. albolabris* from Vallecitos, Guerrero, Mexico.

propose this species to be provisionally classified as Critically Endangered B1ab(iii), based on the IUCN Red List criteria that its occurrence is less than 100 km², it occurs in only one threat-defined location, and there is ongoing decline in the extent and quality of its habitat due to small-scale cattle ranching and maize farming.

The species richness of the subgenus *Syrrhophus* in Guerrero (9 species) represents 27% of the species richness in Mexico (35 species). The number of species known in this state will likely increase as more isolated mountain regions of Guerrero are explored. Guerrero currently has 83 species of amphibians, which represents 20.3% of the approximately 407 species currently recognized for Mexico (AmphibiaWeb 2020). More research in Guerrero is necessary to

continue documenting the incredible biodiversity of this state, as rampant habitat destruction and illegal logging continue to destroy the unique amphibian habitats in the forests of the Sierra Madre del Sur (Lips et al. 2004).

On the Validity of *Eleutherodactylus nebulosus* Taylor, 1943 and *E. rubrimaculatus* Smith and Taylor, 1945 as Species

Based on our phylogenetic results and genetic distances, the populations referred to as “*E. rubrimaculatus*” appear to be conspecific with *E. nebulosus*, as these two species are paraphyletic with respect to each other. Additionally, the genetic distances between the two taxa are very low (less than

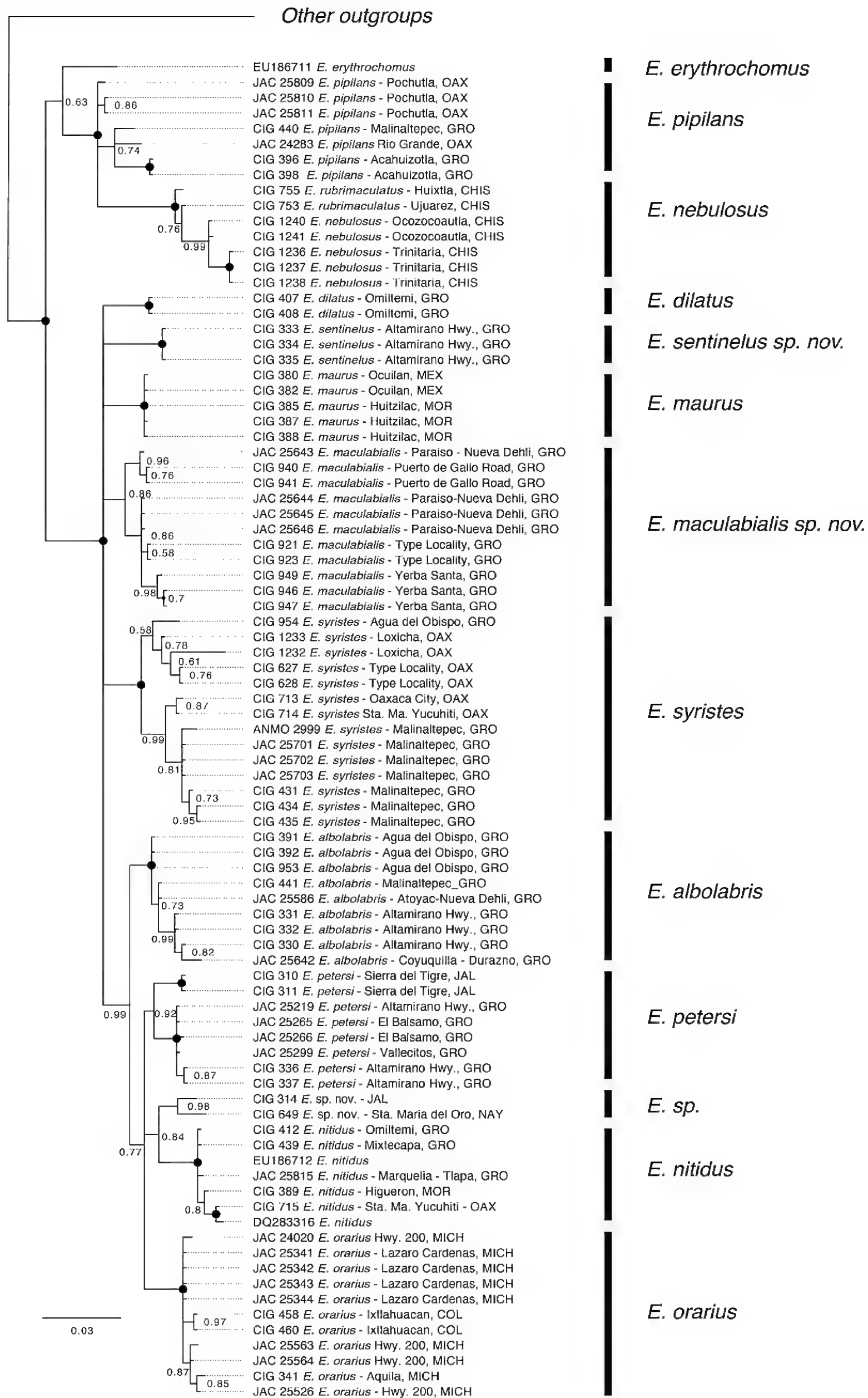


Fig. 12. Bayesian phylogenetic inference of members of the *Eleutherodactylus* subgenus *Syrrhophus*, with a focus on the *E. nitidus* species group, based on the mitochondrial loci 16S rRNA. Black circles represent nodes with a posterior support of 1. All nodes with support of less than 0.5 are collapsed.

Table 5. Uncorrected genetic distances for the 16S rRNA among members of the *Eleutherodactylus nitidus* species group.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|------------------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1. <i>E. rufescens</i> | - | 0.053 | 0.071 | 0.080 | 0.075 | 0.070 | 0.069 | 0.059 | 0.074 | 0.065 | 0.072 | 0.065 | 0.067 | 0.075 |
| 2. <i>E. pipilans</i> | 0.053 | - | 0.037 | 0.040 | 0.052 | 0.051 | 0.056 | 0.048 | 0.058 | 0.055 | 0.055 | 0.050 | 0.052 | 0.061 |
| 3. <i>E. rubrimaculatus</i> | 0.071 | 0.037 | - | 0.013 | 0.076 | 0.066 | 0.072 | 0.062 | 0.069 | 0.079 | 0.073 | 0.074 | 0.069 | 0.082 |
| 4. <i>E. nebulosus</i> | 0.080 | 0.040 | 0.013 | - | 0.072 | 0.064 | 0.071 | 0.062 | 0.065 | 0.073 | 0.066 | 0.067 | 0.063 | 0.070 |
| 5. <i>E. dilatatus</i> | 0.075 | 0.052 | 0.076 | 0.072 | - | 0.044 | 0.033 | 0.026 | 0.038 | 0.035 | 0.030 | 0.037 | 0.027 | 0.042 |
| 6. <i>E. sentinelus</i> sp. nov. | 0.070 | 0.051 | 0.066 | 0.064 | 0.044 | - | 0.033 | 0.031 | 0.040 | 0.042 | 0.043 | 0.037 | 0.043 | 0.055 |
| 7. <i>E. maurus</i> | 0.069 | 0.056 | 0.072 | 0.071 | 0.033 | 0.033 | - | 0.027 | 0.035 | 0.033 | 0.035 | 0.030 | 0.030 | 0.041 |
| 8. <i>E. maculabialis</i> sp. nov. | 0.059 | 0.048 | 0.062 | 0.062 | 0.026 | 0.031 | 0.027 | - | 0.030 | 0.026 | 0.029 | 0.032 | 0.032 | 0.039 |
| 9. <i>E. syristes</i> | 0.074 | 0.058 | 0.069 | 0.065 | 0.038 | 0.040 | 0.035 | 0.030 | - | 0.041 | 0.037 | 0.035 | 0.036 | 0.043 |
| 10. <i>E. albolabris</i> | 0.065 | 0.055 | 0.079 | 0.073 | 0.035 | 0.042 | 0.033 | 0.026 | 0.041 | - | 0.022 | 0.028 | 0.026 | 0.030 |
| 11. <i>E. petersi</i> | 0.072 | 0.055 | 0.073 | 0.066 | 0.030 | 0.043 | 0.035 | 0.029 | 0.037 | 0.022 | - | 0.025 | 0.025 | 0.027 |
| 12. <i>E. sp.</i> | 0.065 | 0.050 | 0.074 | 0.067 | 0.037 | 0.037 | 0.030 | 0.032 | 0.035 | 0.028 | 0.025 | - | 0.025 | 0.027 |
| 13. <i>E. nitidus</i> | 0.067 | 0.052 | 0.069 | 0.063 | 0.027 | 0.043 | 0.030 | 0.032 | 0.036 | 0.026 | 0.025 | 0.025 | - | 0.028 |
| 14. <i>E. orarius</i> | 0.075 | 0.061 | 0.082 | 0.070 | 0.042 | 0.055 | 0.041 | 0.039 | 0.043 | 0.030 | 0.027 | 0.027 | 0.028 | - |

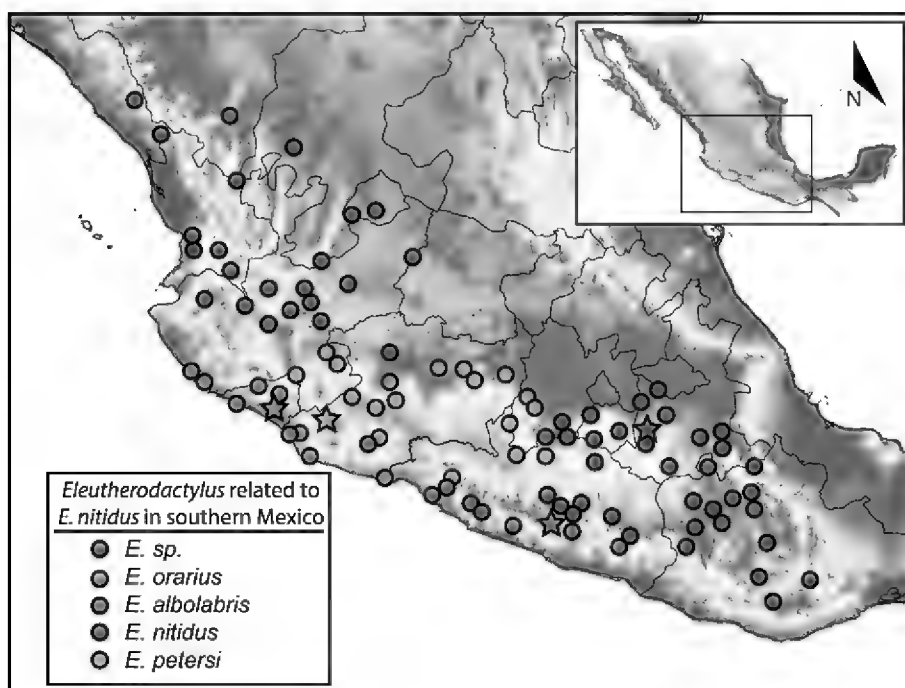


Fig. 13. Map of type localities and distributions of members of the *Eleutherodactylus nitidus* species group. Purple circles represent localities of an undescribed species related to *E. petersi*. For the other four species, stars represent the type localities and circles represent additional localities, which are color coded for species: *E. orarius* (red), *E. albolabris* (blue), *E. nitidus* (green), and *E. petersi* (orange).

1.5%; Table 5).

Taylor (1940) first described *E. nebulosus* from Arriaga, Chiapas, in 1943; and Smith and Taylor (1945) then described “*E. rubrimaculatus*” from Finca La Esperanza, near Escuintla, Chiapas. We did not collect this species at the type locality, however (CIG 755) is near-topotypic, from less than 19 km away on the same slope of the same mountain. The authors differentiated between these species predominately based on size and color pattern. However, those characters appear to be clinal when comparing photos of individual frogs from six localities along Pacific Chiapas (Fig. 14)—from west (Arriaga) to east (Union Juárez) this is evident in the color pattern shifting from the *E. nebulosus* pattern (Arriaga) to the “*E. rubrimaculatus*” pattern (Union Juárez). While molecular material was not available from all the individuals associated with these photos, our analysis presented here did include molecular material from two localities of “*E. rubrimaculatus*” and several localities of *E. nebulosus* around Chiapas. While closely related species of *Syrrhophus* occurring in sympatry or near sympatry normally have very different advertisement calls, populations of *E. nebulosus* at Arriaga, Chiapas, and populations of “*E. rubrimaculatus*” at Huixtla, Chiapas, produce the same single note “peep” (Grünwald, pers. obs.). This suggests they are not reproductively isolated. Furthermore, the genetic distances are very low. (1.1–1.3%; Table 5). We thus conclude that “*E. rubrimaculatus*” is most likely a junior synonym of *E. nebulosus*. Our molecular analysis of frogs related to *E. pipilans* lend support for the recognition of two clades within *E. pipilans*, which are consistent with *E. pipilans* from Guerrero and Oaxaca and *E. nebulosus* + “*E. rubrimaculatus*” from southeastern Oaxaca, Chiapas, and Guatemala (Fig. 7B). Herein we recognize two species, *E. pipilans* and *E. nebulosus*. However, we stress that the lack of genetic sampling

between south-central Oaxaca and northwestern Chiapas may be exacerbating the actual genetic distances between these two populations. We suspect that further sampling around Cerro Quiengola, Tehuantepec, and the Sierra Sacamecate may prove these taxa to be two subspecies of a wide-ranging species.

Common Names for Members of the *Eleutherodactylus nitidus* Species Group

Although species of *Syrrhophus* are often difficult to distinguish, their advertisement calls are useful for distinguishing species in the field. As these frogs are often located during breeding season by following their advertisement calls, it is helpful to know what type of call each species emits. Grünwald et al. (2018) defined vernacular names for the *E. modestus* species group based on the nature of their distinct advertisement calls. Similarly, we propose common names for the species described herein, as well as other species of the *E. nitidus* species group in Appendix 3.

Acknowledgements.—We thank Nadia Pérez-Rivera, Brandon T. La Forest, and André João Grünwald for risking their lives in the sierra of Guerrero and providing valuable assistance in the field. Dr. Vinicius Guerra-Batista of the Centro de Ciências Biológicas e da Natureza at the Universidade Federal do Acre, Brazil, generously donated his time and shared his expertise to help us analyze the advertisement calls of various species of *Eleutherodactylus*. We are indebted to the following persons for allowing us to examine specimens or providing us with digital photographs of preserved specimens under their care: Dr. Adrian Nieto-Montes de Oca, Dr. Oscar Flores-Villela, and Edmundo Pérez-Ramos at MZFC; and Dr. Jonathan Campbell and Dr. Gregory Pandelis at UTA. All specimens which were deposited in MZFC were deposited under permit #FAUT-0093 issued to Dr. Adrian Nieto Montes de Oca. Permits were issued by the Secretaria de Media Ambiente y Recursos Naturales (SEMARNAT). We especially thank Dr. Adrian Nieto Montes de Oca and the Universidad Nacional Autónoma de México, Museo de Zoología de la Facultad de Ciencias, for his generous support in furthering our understanding of the Mexican herpetofauna. We thank Tom J. Devitt and two anonymous reviewers who provided extensive comments, critique, and advice on an earlier version of this manuscript. An extra-special thanks goes to André, Ámbar Lanomy, Emilio, Janelle, and Ximena for sharing their parents’ enthusiasm and love of nature, and for doing field work at such an early age! Biencom Real Estate, Biodiversa A.C., and Herp.mx A.C. provided important funding for the field work.

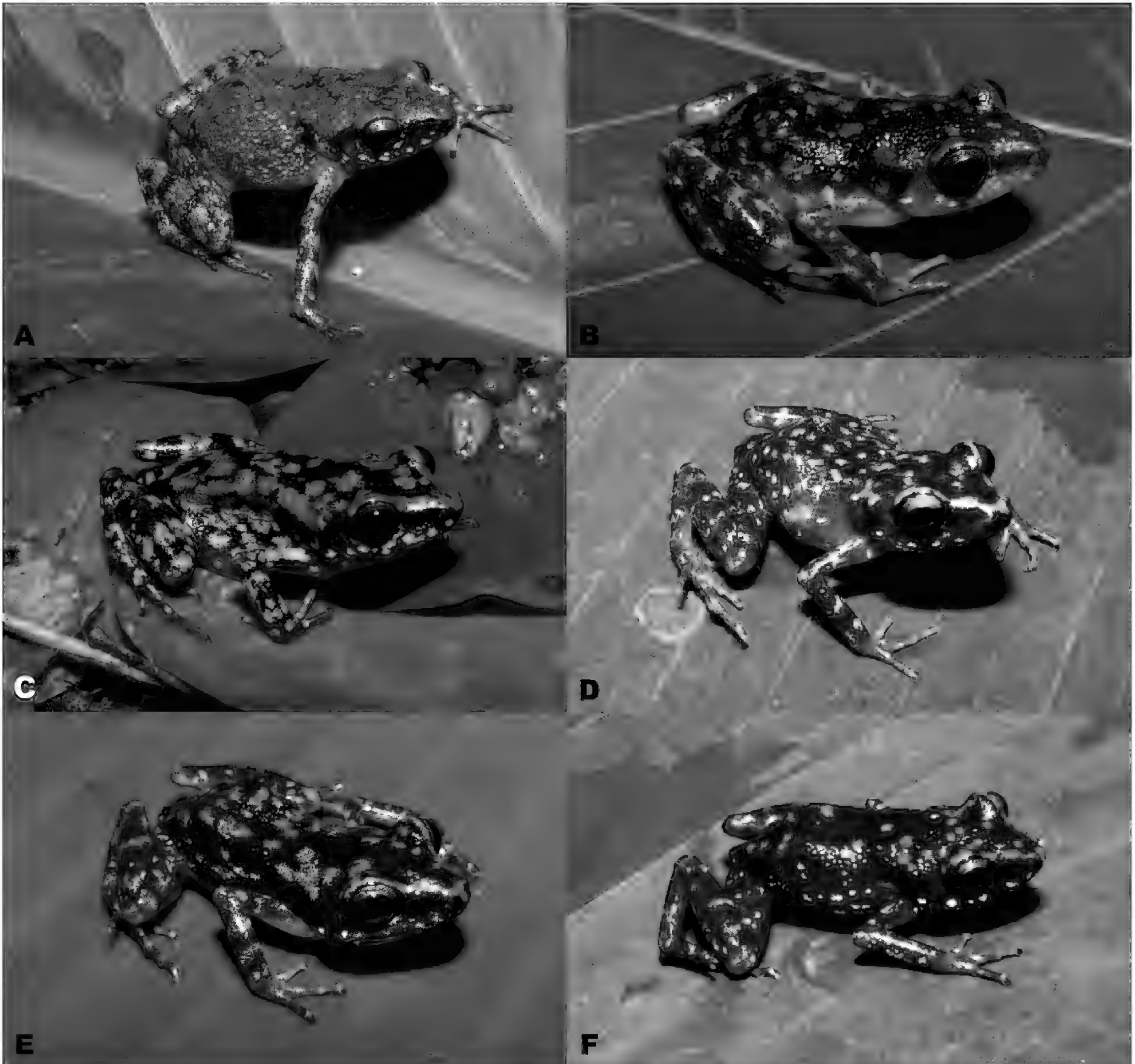


Fig. 14. *Eleutherodactylus nebulosus* in life, including specimens formerly assigned to “*Eleutherodactylus rubrimaculatus*.” (A) *E. nebulosus* from the Municipality of Cintalapa, Chiapas. (B) *E. nebulosus* from the Municipality of Pijijiapan, Chiapas. (C) *E. nebulosus* from the Municipality of Mapastepec, Chiapas. (D) “*E. rubrimaculatus*” (= *E. nebulosus*) from the Municipality of Huixtla, Chiapas. (E) “*E. rubrimaculatus*” (= *E. nebulosus*) from Belisario Dominguez, Chiapas. (F) “*E. rubrimaculatus*” (= *E. nebulosus*) from the Municipality of Union Juárez, Chiapas.

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Jacobo Reyes-Velasco is originally from Colima, Mexico, although he has worked around the world. Jacobo received his Bachelor’s degree in Biology from the Universidad de Guadalajara (CUCBA), and later received his Ph.D. from the University of Texas at Arlington. He is currently leading field expeditions in Mexico, teaching molecular biology, and writing a book on the herpetofauna of Colima. He has published numerous papers on the herpetofauna of western Mexico and is the co-founder of Entorno Biótico A.C. and HERP.MX A.C., two NGOs that focus on conservation initiatives and sustainable development in western Mexico.



Hector Franz-Chávez is a herpetologist and marine mammal specialist originally from Guadalajara, México. Hector Franz is a student of biology at the University of Guadalajara (CUCBA) and has been an avid herpetologist since childhood. His main interests are biogeography, natural history, and ecology of the herpetofauna of Mexico. He is also an avid nature photographer and marine tour guide in the Sea of Cortez, and has collaborated on ten species descriptions as well as numerous herpetological inventories of different parts of Mexico. Currently stationed out of La Paz, Baja California Sur, Hector is working on photographing and documenting the herpetofauna and marine life of the Baja California Peninsula.



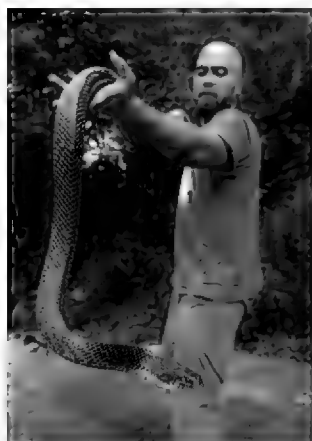
Karen I. Morales-Flores is a herpetologist originally from Guadalajara, Mexico, but she grew up in the United States where she developed an appreciation for nature, and specifically the reptiles in the deserts of Nevada. A student of biology at the University of Guadalajara (CUCBA), Karen (or “Kim”) has participated in numerous field expeditions with the HERP.MX Field Team. Her skills in the laboratory have encouraged her to take on ambitious projects like measuring every external body part of 500 direct-developing frogs. Her research has resulted in the description of nine new species so far, with many more to come. Kim’s ambitions as a herpetologist are only matched by her ambitions as an explorer, and she is currently travelling the world looking for exciting research opportunities.



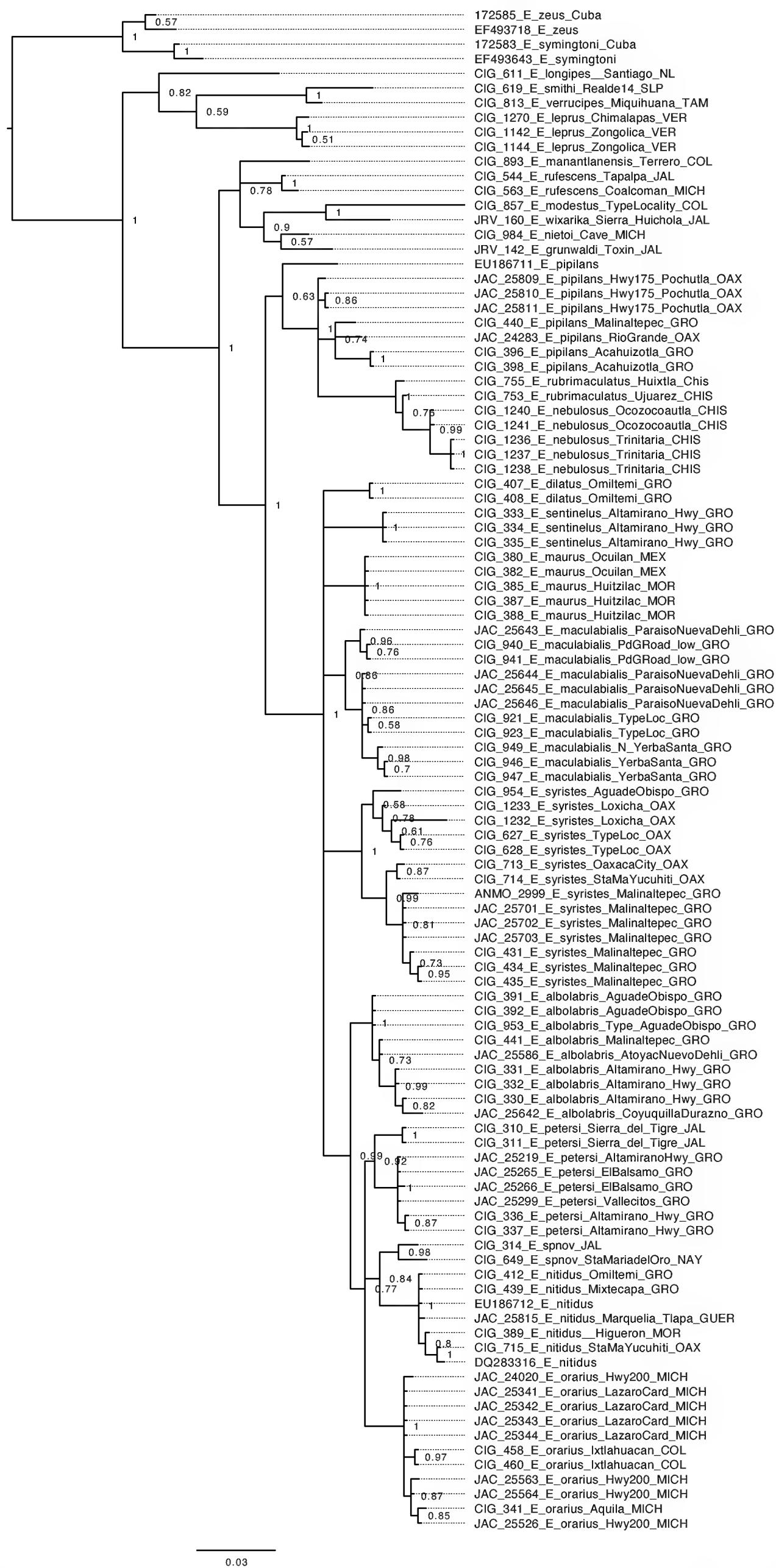
Ivan T. Ahumada-Carrillo is a Mexican herpetologist from Guadalajara, who received his degree from the University of Guadalajara (CUCBA). Ivan is currently an independent investigator who focuses on the biogeography of reptiles and amphibians in western Mexico. He has documented dozens of range extensions and state records, and has authored and co-authored various papers on biogeography, as well as the book *Anfibios y Reptiles del Bosque La Primavera*. Another interest of his is wildlife photography, and his work has been published throughout Mexico in educational materials, web sites, scientific magazines, and books. Ivan has now co-authored 11 new species descriptions, as well as numerous range extensions and state records from Mexico.



Christopher M. Rodriguez is a herpetologist from Los Angeles, California, who studied biology at California State University. Chris is an avid breeder of endangered reptiles and amphibians. Working at the Los Angeles Zoo, Chris has led captive breeding projects for endangered herpetofauna from around the world, as well as extremely delicate local species such as the Mountain Yellow-legged Frog (*Rana muscosa*). When not saving species, Chris has led field expeditions around the world, including Madagascar, Indonesia, Thailand, and above all Mexico. As a member of the HERP.MX Field Team, Chris has helped with the initial field work for several of the new species the Team has discovered.



Jason M. Jones was born and raised in southern California, where he studied biology and computer science at the University of California, Irvine. Currently residing in Colima, he has spent the past 17 years studying and photographing the herpetofauna of Mexico. A specialist in Mexican pitvipers, Jason co-led the rediscovery of *Crotalus lannomi*, and collaborated in the recent descriptions of *Crotalus campbelli*, *Crotalus tlaloci*, and *Ophryacus smaragdinus*. Jason co-founded HERP.MX which, in collaboration with Biodiversa, A.C., is currently developing strategies for the conservation of at-risk reptile species.



Supplementary Fig. 1. Bayesian phylogenetic inference of members of the *Eleutherodactylus* subgenus *Syrrhophus*, based on the mitochondrial loci 16S rRNA. All nodes with support of less than 0.5 are collapsed.

Two new *Eleutherodactylus* species from Mexico

Appendix 1. List of subgenus *Syrrhophus* specimens examined in this study. Museum codes: MZFC = Museo de Zoología de la Facultad de Ciencias, Universidad Autónoma de México (UNAM); UTA = Amphibian and Reptile Diversity Research Center, University of Texas at Arlington. Field number codes: ANMO = Adrian Nieto Montes de Oca, uncatalogued at MZFC; CIG = Chris Grünwald, uncatalogued at MZFC; JAC = Jonathan A. Campbell, uncatalogued at UTA; JHM = John Malone, uncatalogued at UTA; JRV = Jacobo Reyes-Velasco, uncatalogued at MZFC.

Specimens Examined ($n = 495$)

- Eleutherodactylus albolabris* ($n = 20$): MEXICO: Guerrero: MZFC 33025–33030 (CIG 00327–00332), 33082–33085 (CIG 00390–00393), MZFC 33108–33109 (CIG 00441–00442), MZFC 33230 (CIG 00668), MZFC 33300–33301 (CIG 00903–00904), MZFC 33323 (CIG 00953), MZFC 33325–33326 (CIG 00955–00956), JAC 25586, 25642.
- Eleutherodactylus angustidigitum* ($n = 20$): MEXICO: Jalisco: MZFC 33127–33130 (CIG 00476–00479), MZFC 33224–33225 (CIG 00662–00663), MZFC 33386–33388 (CIG 00991–00993), JAC 24912; Michoacán: MZFC 33015–33017 (CIG 00316–00318), MZFC 33065–33070 (CIG 00373–00378), JAC 26977.
- Eleutherodactylus campi* ($n = 13$): MEXICO: Nuevo León: MZFC 33195–33198 (CIG 00606–00609); UNITED STATES: Texas: JHM 1390–1394.
- Eleutherodactylus colimotl* ($n = 20$): MEXICO: Colima: MZFC 29282 (CIG 00468), MZFC 33115–33120 (CIG 00462–00467), MZFC 33237–33239 (CIG 00682–00684), MZFC 33299 (CIG 00901), MZFC 33329–33330 (CIG 00960–00961), JAC 30498–30499, 30631; Michoacán: MZFC 33036 (CIG 00340), JAC 23999–24001.
- Eleutherodactylus cystignathoides* ($n = 6$): MEXICO: Veracruz: MZFC 33351–33353 (CIG 01163–01165), MZFC 33354 (CIG 01170), JAC 30000–30001.
- Eleutherodactylus dennisi* ($n = 13$): MEXICO: Tamaulipas: MZFC 33255–33261 (CIG 00822–00828), UTA 59516–59521.
- Eleutherodactylus dilatus* ($n = 19$): MEXICO: Guerrero: MZFC 33089–33094 (CIG 00405–00410), MZFC 33097 (CIG 00428), MZFC 33231 (CIG 00669), UTA 4017–4020, 4023–4024, 5269, 5276–5279.
- Eleutherodactylus erendirae* ($n = 25$): MEXICO: Jalisco: MZFC 33000–33008 (CIG 00300–00309), MZFC 33226–33229 (CIG 00664–00667), MZFC 33232 (CIG 00673), MZFC 33234–33235 (CIG 00679–00681); Michoacán: MZFC 29274, 33019–33024 (CIG 00319–00325).
- Eleutherodactylus floresvillelai* ($n = 12$): MEXICO: Michoacán: MZFC 33053–33064 (CIG 00361–00372).
- Eleutherodactylus grandis* ($n = 1$): MEXICO: Ciudad de Mexico: UTA 56845.
- Eleutherodactylus grunwaldi* ($n = 12$): MEXICO: Colima: MZFC 27467–27475, MZFC 27484, MZFC 33298 (CIG 00898); JRV 00230.
- Eleutherodactylus guttilatus* ($n = 10$): MEXICO: Guanajuato: MZFC 33367–33369 (CIG 01248–01250); San Luis Potosí: MZFC 33200–33206 (CIG 00619–00625).
- Eleutherodactylus interorbitalis* ($n = 7$): MEXICO: Sinaloa: MZFC 33186–33187 (CIG 00584–00585), MZFC 33190–33194 (CIG 00600–00604).
- Eleutherodactylus jaliscoensis* ($n = 15$): MEXICO: Jalisco: MZFC 33131–33141 (CIG 00480–00490), MZFC 33274–33276 (CIG 00861–00863), MZFC 33280 (CIG 00876).
- Eleutherodactylus leprus* ($n = 7$): MEXICO: Veracruz: MZFC 33345–33350 (CIG 01139–01144), CIG 01270.
- Eleutherodactylus longipes* ($n = 3$): MEXICO: Nuevo León: MZFC 33199 (CIG 00611); Querétaro: UTA 59421–59422.
- Eleutherodactylus maculabialis* sp. nov. ($n = 27$): MEXICO: Guerrero: MZFC 33307–33319 (CIG 00916–00923, 00940–00941, 00945–00947), MZFC 33321 (CIG 00949), MZFC 33323 (CIG 00953), CIG 01484–01485, 01501, JAC 25643–25646.
- Eleutherodactylus marnocki* ($n = 3$): USA: Texas: JHM 1427–1429.
- Eleutherodactylus manantlanensis* ($n = 14$): MEXICO: Colima: MZFC 33372–33377 (CIG 00530–00535), MZFC 33379–33381 (CIG 00646–00648), MZFC 33292–33296 (CIG 00892–00896).
- Eleutherodactylus maurus* ($n = 11$): MEXICO: Estado de México: MZFC 33071–33076 (CIG 00379–00384), MZFC 33355 (CIG 01174); Morelos: MZFC 33077–33080 (CIG 00385–00388).
- Eleutherodactylus modestus* ($n = 34$): MEXICO: Colima: MZFC 26888–26889, MZFC 33263–33270 (CIG 00850–00857), MZFC 33291 (CIG 00891), MZFC 33297 (CIG 00897); Jalisco: MZFC 33144–33149 (CIG 00493–00498), MZFC 33150–33154 (CIG 00505–00509), MZFC 33161 (CIG 00522), MZFC 33183–33185 (CIG 00570–00572), MZFC 33217–33223 (00655–00661).
- Eleutherodactylus nebulosus* ($n = 9$): MEXICO: Chiapas: MZFC 33249–33251 (CIG 00753, 00755–00756), MZFC 33361–33366 (CIG 01236–01241).
- Eleutherodactylus nietoi* ($n = 13$): MEXICO: Michoacán: MZFC 33121 (CIG 00299), MZFC 33042–33045 (CIG 00346–00349), MZFC 33050–33052 (CIG 00355–00357), MZFC 33336–33337 (CIG 00974–00975), MZFC 33342–33343 (CIG 00983–00984), MZFC 33344 (CIG 00994).
- Eleutherodactylus nitidus* ($n = 31$): MEXICO: Estado de México: JAC 27237; Guerrero: MZFC 33096–33097 (CIG 00411–00412), MZFC 33104–33105 (CIG 00437–00438), JAC 25815; Morelos: MZFC 33081 (CIG 00389); Oaxaca: MZFC 33357–33358 (CIG 01211–01212); Puebla: MZFC 33356 (CIG 01181), JAC 27256–27276.
- Eleutherodactylus orarius* ($n = 13$): MEXICO: Colima: MZFC 26890, MZFC 33262 (CIG 00849); Michoacán: MZFC 33037 (CIG 00341), MZFC 33335 (CIG 00973), JAC 24020, 25526, 25563–25564, 29107, 30500–30501, 30517, 30625.
- Eleutherodactylus pallidus* ($n = 13$): MEXICO: Jalisco: MZFC 33271–33272 (CIG 00858–00859); Nayarit: MZFC 33189 (CIG 00588), MZFC 33212–33216 (CIG 00650–00654), MZFC 33243–33245 (CIG 00688–00690), MZFC 33018 (CIG 00995); Sinaloa: MZFC 33188 (CIG 00586).
- Eleutherodactylus petersi* ($n = 25$): MEXICO: Guerrero: MZFC 33034–33035 (CIG 00336–00337); JAC 25219, 25265–25266, 25299; Jalisco: MZFC 33010–33014 (CIG 00310–00314), MZFC 33034–33035 (CIG 00336–00337), MZFC 33110 (CIG

00457), MZFC 33273 (CIG 00860), JAC 28612; Michoacán: MZFC 33382–33385 (CIG 00675–00677), JAC 26947; Nayarit: MZFC 33211 (CIG 00649), MZFC 33240–33242 (CIG 00685–00687).

Eleutherodactylus pipilans ($n = 15$): MEXICO: Guerrero: MZFC 33086–33088 (CIG 00396–00398), MZFC 33106–33107 (CIG 00439–00440), MZFC 33322 (CIG 00952), CIG 1465; Oaxaca: MZFC 33210 (CIG 00645), JAC 24283, 25809–25811.

Eleutherodactylus rufescens ($n = 40$): MEXICO: Jalisco: MZFC 33122–33126 (CIG 00471–00475), MZFC 33162–33164 (CIG 00527–00529), MZFC 33165–33174 (CIG 00544–00553), MZFC 33385 (CIG 00678); Michoacán: MZFC 33038–33041 (CIG 00342–00345), MZFC 33046–33049 (CIG 00350–00353), MZFC 33175–33182 (CIG 00559–00566), MZFC 33233 (CIG 00674), MZFC 33338 (CIG 00976), MZFC 33339–33341 (CIG 00980–00982).

Eleutherodactylus saxatilis ($n = 4$): MEXICO: Sinaloa: MZFC 26893, 26896, 26898–26899.

***Eleutherodactylus sentinelus* sp. nov.** ($n = 8$): MEXICO: Guerrero: MZFC 33031–33033 (CIG 00333–00335), MZFC 33302–33306 (CIG 00907–00913).

Eleutherodactylus syristes ($n = 21$): MEXICO: Guerrero: ANMO 2999; MZFC 33098–33103 (CIG 00431–00436), MZFC 33324 (CIG 00954), MZFC 33327–33328 (CIG 00957–00958) JAC 25701–25703; Oaxaca: MZFC 33207–33208 (CIG 00627–00628), MZFC 33209 (CIG 00644), 33378 (CIG00643), MZFC 33246–33247 (CIG 00713–00714), MZFC 33359–33360 (CIG 01232–01233).

Eleutherodactylus teretistes ($n = 5$): MEXICO: Jalisco: MZFC 33142–33143 (CIG 00491–00492), MZFC 33277–33279 (CIG 00864–00866).

Eleutherodactylus verrucipes ($n = 3$): MEXICO: MZFC 33253–33254 (CIG 00813–00814), CIG 01273.

Eleutherodactylus wixarika ($n = 3$): MEXICO: Jalisco: MZFC 27477–27479.

Two new *Eleutherodactylus* species from Mexico

Appendix 2. Specimen information and GenBank accession numbers.

| Field number | Species | Museum number | Locality | GenBank number |
|--------------|---|---------------|---------------------|----------------|
| — | <i>Eleutherodactylus symingtoni</i> | — | Cuba: Pinar del Río | EF493643 |
| — | <i>Eleutherodactylus nitidus</i> | AMCC118239 | Mexico: Puebla | EU186712 |
| — | <i>Eleutherodactylus erythrochomus</i> | MZFC 16254 | Mexico: Guerrero | EU186711 |
| — | <i>Eleutherodactylus zeus</i> | USNM335740 | Cuba: Pinar del Río | EF493718 |
| ANMO2999 | <i>Eleutherodactylus syristes</i> | — | Mexico: Guerrero | MT872423 |
| CIG1142 | <i>Eleutherodactylus leprus</i> | MZFC33348 | Mexico: Veracruz | MT872424 |
| CIG1144 | <i>Eleutherodactylus leprus</i> | MZFC33350 | Mexico: Veracruz | MT872425 |
| CIG1232 | <i>Eleutherodactylus syristes</i> | MZFC33359 | Mexico: Oaxaca | MT872426 |
| CIG1233 | <i>Eleutherodactylus syristes</i> | MZFC33360 | Mexico: Oaxaca | MT872427 |
| CIG1236 | <i>Eleutherodactylus nebulosus</i> | MZFC33361 | Mexico: Chiapas | MT872428 |
| CIG1237 | <i>Eleutherodactylus nebulosus</i> | MZFC33362 | Mexico: Chiapas | MT872429 |
| CIG1238 | <i>Eleutherodactylus nebulosus</i> | MZFC33363 | Mexico: Chiapas | MT872430 |
| CIG1240 | <i>Eleutherodactylus nebulosus</i> | MZFC33365 | Mexico: Chiapas | MT872431 |
| CIG1241 | <i>Eleutherodactylus nebulosus</i> | MZFC33366 | Mexico: Chiapas | MT872432 |
| CIG1270 | <i>Eleutherodactylus leprus</i> | — | Mexico: Veracruz | MT872433 |
| CIG310 | <i>Eleutherodactylus petersi</i> | MZFC33010 | Mexico: Jalisco | MT872487 |
| CIG311 | <i>Eleutherodactylus nitidus</i> | MZFC33011 | Mexico: Jalisco | MG857033 |
| CIG314 | <i>Eleutherodactylus nitidus</i> | MZFC33014 | Mexico: Jalisco | MG857034 |
| CIG330 | <i>Eleutherodactylus albolabris</i> | MZFC33028 | Mexico: Guerrero | MT872481 |
| CIG331 | <i>Eleutherodactylus albolabris</i> | MZFC33029 | Mexico: Guerrero | MT872482 |
| CIG332 | <i>Eleutherodactylus albolabris</i> | MZFC33030 | Mexico: Guerrero | MT872483 |
| CIG333 | <i>Eleutherodactylus sentinelus</i> sp. nov. | MZFC33031 | Mexico: Guerrero | MT872484 |
| CIG334 | <i>Eleutherodactylus sentinelus</i> sp. nov. | MZFC33032 | Mexico: Guerrero | MT872485 |
| CIG335 | <i>Eleutherodactylus sentinelus</i> sp. nov. | MZFC33033 | Mexico: Guerrero | MT872486 |
| CIG336 | <i>Eleutherodactylus nitidus</i> | MZFC33034 | Mexico: Guerrero | MG857032 |
| CIG337 | <i>Eleutherodactylus petersi</i> | MZFC33035 | Mexico: Guerrero | MT872473 |
| CIG341 | <i>Eleutherodactylus orarius</i> | MZFC33037 | Mexico: Michoacán | MG857041 |
| CIG380 | <i>Eleutherodactylus maurus</i> | MZFC33072 | Mexico: Mexico | MG857011 |
| CIG382 | <i>Eleutherodactylus maurus</i> | MZFC33074 | Mexico: Mexico | MT872478 |
| CIG385 | <i>Eleutherodactylus maurus</i> | MZFC33077 | Mexico: Morelos | MT872479 |
| CIG387 | <i>Eleutherodactylus maurus</i> | MZFC33079 | Mexico: Morelos | MT872480 |
| CIG388 | <i>Eleutherodactylus maurus</i> | MZFC33080 | Mexico: Morelos | MG857010 |
| CIG389 | <i>Eleutherodactylus nitidus</i> | MZFC33081 | Mexico: Morelos | MG857029 |
| CIG391 | <i>Eleutherodactylus albolabris</i> | MZFC33083 | Mexico: Guerrero | MG856955 |
| CIG392 | <i>Eleutherodactylus albolabris</i> | MZFC33084 | Mexico: Guerrero | MT872468 |
| CIG396 | <i>Eleutherodactylus pipilans</i> | MZFC33086 | Mexico: Guerrero | MG857054 |
| CIG398 | <i>Eleutherodactylus pipilans</i> | MZFC33088 | Mexico: Guerrero | MG857055 |
| CIG407 | <i>Eleutherodactylus dilatus</i> | MZFC33091 | Mexico: Guerrero | MG856973 |
| CIG408 | <i>Eleutherodactylus dilatus</i> | MZFC33092 | Mexico: Guerrero | MG856974 |
| CIG412 | <i>Eleutherodactylus nitidus</i> | MZFC33096 | Mexico: Guerrero | MG857031 |
| CIG431 | <i>Eleutherodactylus syristes</i> | MZFC33098 | Mexico: Guerrero | MT872471 |
| CIG434 | <i>Eleutherodactylus syristes</i> | MZFC33101 | Mexico: Guerrero | MT872472 |
| CIG435 | <i>Eleutherodactylus syristes</i> | MZFC33102 | Mexico: Guerrero | MG857071 |
| CIG439 | <i>Eleutherodactylus nitidus</i> | MZFC33106 | Mexico: Guerrero | MT872474 |
| CIG440 | <i>Eleutherodactylus pipilans</i> | MZFC33107 | Mexico: Guerrero | MT872475 |

Appendix 2 continued. Specimen information and GenBank accession numbers.

| Field number | Species | Museum number | Locality | GenBank number |
|--------------|---|---------------|-------------------------|----------------|
| CIG441 | <i>Eleutherodactylus albolabris</i> | MZFC33108 | Mexico: Guerrero | MT872476 |
| CIG458 | <i>Eleutherodactylus orarius</i> | MZFC33111 | Mexico: Colima | MT872477 |
| CIG460 | <i>Eleutherodactylus orarius</i> | MZFC33113 | Mexico: Colima | MG857042 |
| CIG544 | <i>Eleutherodactylus rufescens</i> | MZFC33165 | Mexico: Jalisco | MG857039 |
| CIG563 | <i>Eleutherodactylus rufescens</i> | MZFC33179 | Mexico: Michoacán | MG857060 |
| CIG611 | <i>Eleutherodactylus longipes</i> | MZFC33199 | Mexico: Nuevo Leon | MG857006 |
| CIG619 | <i>Eleutherodactylus guttilatus</i> | MZFC33200 | Mexico: San Luis Potosí | MG856994 |
| CIG627 | <i>Eleutherodactylus syristes</i> | MZFC33207 | Mexico: Oaxaca | MT872467 |
| CIG628 | <i>Eleutherodactylus syristes</i> | MZFC33208 | Mexico: Oaxaca | MG857073 |
| CIG649 | <i>Eleutherodactylus</i> sp. nov. | MZFC33211 | Mexico: Nayarit | MT872469 |
| CIG713 | <i>Eleutherodactylus syristes</i> | MZFC33246 | Mexico: Oaxaca | MT872470 |
| CIG714 | <i>Eleutherodactylus syristes</i> | MZFC33247 | Mexico: Oaxaca | MG857072 |
| CIG715 | <i>Eleutherodactylus nitidus</i> | MZFC33248 | Mexico: Oaxaca | MG857030 |
| CIG753 | <i>Eleutherodactylus nebulosus</i> | MZFC33249 | Mexico: Chiapas | MG857056 |
| CIG755 | <i>Eleutherodactylus nebulosus</i> | MZFC33250 | Mexico: Chiapas | MG857057 |
| CIG813 | <i>Eleutherodactylus verrucipes</i> | MZFC33253 | Mexico: Tamaulipas | MG857079 |
| CIG857 | <i>Eleutherodactylus modestus</i> | MZFC33270 | Mexico: Colima | MG857021 |
| CIG893 | <i>Eleutherodactylus manantlanensis</i> | MZFC33293 | Mexico: Colima | MG857007 |
| CIG921 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33312 | Mexico: Guerrero | MT872460 |
| CIG923 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33314 | Mexico: Guerrero | MT872461 |
| CIG940 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33315 | Mexico: Guerrero | MT872462 |
| CIG941 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33316 | Mexico: Guerrero | MT872463 |
| CIG946 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33318 | Mexico: Guerrero | MT872464 |
| CIG947 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33319 | Mexico: Guerrero | MT872465 |
| CIG949 | <i>Eleutherodactylus maculabialis</i> sp. nov. | MZFC33321 | Mexico: Guerrero | MT872466 |
| CIG953 | <i>Eleutherodactylus albolabris</i> | MZFC33323 | Mexico: Guerrero | MG856956 |
| CIG954 | <i>Eleutherodactylus syristes</i> | MZFC33324 | Mexico: Guerrero | MG857070 |
| CIG984 | <i>Eleutherodactylus nietoi</i> | MZFC33343 | Mexico: Michoacán | MG857028 |
| JAC24020 | <i>Eleutherodactylus orarius</i> | UTAA59508 | Mexico: Michoacán | MT872434 |
| JAC24283 | <i>Eleutherodactylus pipilans</i> | UTAA64104 | Mexico: Oaxaca | MT872435 |
| JAC25219 | <i>Eleutherodactylus petersi</i> | UTAA61561 | Mexico: Guerrero | MT872436 |
| JAC25265 | <i>Eleutherodactylus petersi</i> | UTAA61562 | Mexico: Guerrero | MT872437 |
| JAC25266 | <i>Eleutherodactylus petersi</i> | UTAA61563 | Mexico: Guerrero | MT872438 |
| JAC25299 | <i>Eleutherodactylus petersi</i> | UTAA61568 | Mexico: Guerrero | MT872439 |
| JAC25341 | <i>Eleutherodactylus orarius</i> | UTAA62400 | Mexico: Michoacán | MT872440 |
| JAC25342 | <i>Eleutherodactylus orarius</i> | UTAA62401 | Mexico: Michoacán | MT872441 |
| JAC25343 | <i>Eleutherodactylus orarius</i> | UTAA62402 | Mexico: Michoacán | MT872442 |
| JAC25344 | <i>Eleutherodactylus orarius</i> | UTAA62403 | Mexico: Michoacán | MT872443 |
| JAC25526 | <i>Eleutherodactylus orarius</i> | UTAA62090 | Mexico: Michoacán | MT872444 |
| JAC25563 | <i>Eleutherodactylus orarius</i> | UTAA61575 | Mexico: Michoacán | MT872445 |
| JAC25564 | <i>Eleutherodactylus orarius</i> | UTAA61576 | Mexico: Michoacán | MT872446 |

Two new *Eleutherodactylus* species from Mexico

Appendix 2 continued. Specimen information and GenBank accession numbers.

| Field number | Species | Museum number | Locality | GenBank number |
|--------------|--|---------------|------------------|----------------|
| JAC25586 | <i>Eleutherodactylus albolabris</i> | UTAA61577 | Mexico: Guerrero | MT872447 |
| JAC25642 | <i>Eleutherodactylus albolabris</i> | UTAA61578 | Mexico: Guerrero | MT872448 |
| JAC25643 | <i>Eleutherodactylus maculabialis</i> sp. nov. | UTAA62091 | Mexico: Guerrero | MT872449 |
| JAC25644 | <i>Eleutherodactylus maculabialis</i> sp. nov. | UTAA64131 | Mexico: Guerrero | MT872450 |
| JAC25645 | <i>Eleutherodactylus maculabialis</i> sp. nov. | UTAA64130 | Mexico: Guerrero | MT872451 |
| JAC25646 | <i>Eleutherodactylus maculabialis</i> sp. nov. | — | Mexico: Guerrero | MT872452 |
| JAC25701 | <i>Eleutherodactylus syristes</i> | UTAA61580 | Mexico: Guerrero | MT872453 |
| JAC25702 | <i>Eleutherodactylus syristes</i> | UTAA61581 | Mexico: Guerrero | MT872454 |
| JAC25703 | <i>Eleutherodactylus syristes</i> | UTAA61582 | Mexico: Guerrero | MT872455 |
| JAC25809 | <i>Eleutherodactylus pipilans</i> | UTAA62404 | Mexico: Oaxaca | MT872456 |
| JAC25810 | <i>Eleutherodactylus pipilans</i> | UTAA62405 | Mexico: Oaxaca | MT872457 |
| JAC25811 | <i>Eleutherodactylus pipilans</i> | UTAA62406 | Mexico: Oaxaca | MT872458 |
| JAC25815 | <i>Eleutherodactylus nitidus</i> | UTAA61584 | Mexico: Guerrero | MT872459 |
| JRV142 | <i>Eleutherodactylus grunwaldi</i> | — | Mexico: Jalisco | MG856993 |
| JRV160 | <i>Eleutherodactylus wixarika</i> | MZFZ27477 | Mexico: Jalisco | MG857081 |

Appendix 3. Proposed standardized common names for the *Eleutherodactylus nitidus* species group members.

| | |
|---|------------------------------|
| <i>Eleutherodactylus albolabris</i> | White-lipped Whistling Frog |
| <i>Eleutherodactylus dilatus</i> | Omitemi Peeping Frog |
| <i>Eleutherodactylus erythrochomus</i> | Tierra Colorada Peeping Frog |
| <i>Eleutherodactylus maurus</i> | Dusky Piping Frog |
| <i>Eleutherodactylus nitidus</i> | Shiny Whistling Frog |
| <i>Eleutherodactylus orarius</i> | Coastal Whistling Frog |
| <i>Eleutherodactylus petersi</i> | Peters’ Whistling Frog |
| <i>Eleutherodactylus pipilans</i> | Guerrero Peeping Frog |
| <i>Eleutherodactylus nebulosus</i> | Clouded Peeping Frog |
| <i>Eleutherodactylus maculabialis</i> sp. nov. | Spot-lipped Trilling Frog |
| <i>Eleutherodactylus sentinelus</i> sp. nov. | El Balsamo Peeping Frog |
| <i>Eleutherodactylus syristes</i> | Oaxaca Trilling Frog |



The distribution and conservation status of the Dwarf Marsupial Frog (*Flectonotus fitzgeraldi*, Anura, Hemiphractidae) in Trinidad, Tobago, and Venezuela

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Abstract.— The Dwarf Marsupial Frog, *Flectonotus fitzgeraldi* (family Hemiphractidae), has been reported to occur only in Trinidad, Tobago, and the Paria Range of Venezuela. This species is listed as Endangered on the IUCN Red List, based on its small geographic distribution and the fragmentation of its habitat, which is said to be declining both in extent and quality. Using molecular methods, we confirm herein that the three populations do belong to the same species. However, extensive presence/absence and focused population surveys show that the frog's distribution is more extensive than previously reported in both Trinidad and Venezuela. In Trinidad and Tobago, the frog is abundant in forests wherever its host plants occur, notably the bromeliad *Heliconia bihai* (Balisier in Trinidad; Bijao in Venezuela) and the aroid *Xanthosoma jacquinii* (Elephant's Ear). In Venezuela, the species is frequently found where there is suitable habitat, but an exhaustive population study is needed to diagnose its current situation. No evidence was found of habitat decline in Trinidad and Tobago, but in Venezuela the loss of habitat is evident, mainly because of subsistence agricultural activities, which have been developing in northeast Venezuela since at least 1930. The Red List status of this species is in need of revision.

Keywords. Amphibia, habitat loss, IUCN Red List, phytotelmata, southern Caribbean

Resumen.— La ranita marsupial *Flectonotus fitzgeraldi* (familia Hemiphractidae), se conoce solo de Trinidad, Tobago y la Región de Paria en Venezuela. La Lista Roja de la UICN cataloga esta especie como En Peligro, con base a su área de distribución geográfica reducida y a la fragmentación de su hábitat, el cual se reduce progresivamente tanto en su extensión como en su calidad. Usando métodos moleculares comparativos, en este trabajo se confirma que las tres poblaciones pertenecen a una misma especie. Sin embargo, un estudio poblacional y de presencia/ausencia demuestra que la distribución geográfica de este anfibio es más amplia que la señalada anteriormente, principalmente en Trinidad y en Venezuela. En Trinidad y Tobago, esta rana es frecuente en áreas boscosas siempre que sus plantas huéspedes estén presentes, principalmente bromelias, *Heliconia bihai* (balisier en Trinidad; bijao en Venezuela) y *Xanthosoma jacquinii* (oreja de elefante). En Venezuela, la especie es frecuente, pero se requiere un estudio poblacional más exhaustivo para diagnosticar con precisión su situación. No se encontró evidencia de un deterioro importante en la calidad de su hábitat en Trinidad y Tobago, pero en Venezuela la pérdida de hábitat es evidente, principalmente como resultado de las actividades agrícolas de subsistencia, que se desarrollan en el noroeste de Venezuela al menos desde 1930. El estado de esta especie en la Lista Roja precisa de una revisión.

Palabras clave. Anfibia, pérdida de hábitat, Lista roja IUCN, fitotelmata, Sur del Caribe

Citation: Smith J, Jowers MJ, Auguste RJ, Hoskisson P, Beyts C, Muir GM, Greener MS, Thornham D, Byrne I, Lehtinen R, Eyre M, Rutherford MG, Murphy JC, De Freitas M, Rivas GA, Downie JR. 2021. The distribution and conservation status of the Dwarf Marsupial Frog (*Flectonotus fitzgeraldi*, Anura, Hemiphractidae) in Trinidad, Tobago, and Venezuela. *Amphibian & Reptile Conservation* 15(1) [General Section]: 36–56 (e273).

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Accepted: 29 September 2020; **Published:** 30 June 2021

Introduction

The neotropical frog family Hemiphractidae includes six tree frog genera (118 species described so far; Frost 2020), in which females incubate small clutches of large eggs on their backs, either openly (in *Stefania* and *Cryptobatrachus*) or in a more or less closed cutaneous pouch (all other genera). One member of a two-species genus, the Dwarf Marsupial Frog *Flectonotus fitzgeraldi* (Parker 1934), is found in Trinidad, Tobago, and the nearby Paria Biota region of Venezuela, which includes the Serrania de Paria, Cerros Campeare, and La Cerbatana. In this small species (maximum snout-vent length in males 21 mm and in females 25 mm), developing individuals (clutch size 2–6) hatch as late-stage larvae and are deposited by the female into phytotelmata, which are small bodies of water enclosed by leaves, such as bromeliad ‘tanks.’ These larvae do not feed but subsist on the remaining yolk (Kenny 1969) and soon enter the process of metamorphosis, which is indicated by forelimb emergence. Downie et al. (2004) found that metamorphosis was complete (tail reabsorption) after 4.5 ± 0.7 days. Duellman and Gray (1983) suggested that individual *Flectonotus* females were capable of producing several egg clutches in a year, but data are still needed to test this suggestion for *F. fitzgeraldi*. *Flectonotus fitzgeraldi* are arboreal at night, with males calling from leaves such as those of bromeliads and *Heliconia bihai*, which is said to occur primarily during a period of about one hour, from soon before until soon after sunset (Murphy 1997). During the day, they may be active in leaf litter on the ground (Duellman and Gray 1983).

Flectonotus fitzgeraldi was assessed as Endangered by La Marca et al. (2004) for the IUCN Red List, based on criteria B1ab(iii), on the grounds that its “extent of occurrence is less than 5,000 km², its distribution is severely fragmented, and that there is continuing decline in the extent and quality of its habitat” in all three regions. Its population status was judged to be declining. However, this assessment appears not to have been based on published research and included the statement that “further work is needed to establish the current population status of this species.”

In the past, many anuran species were listed as occurring in Trinidad, Tobago, and northern Venezuela. However, modern assessments using molecular methods have not always supported these patterns. For example, the arobobatid *Mannophryne trinitatis* is now known to occur only in Trinidad, with the Venezuelan and Tobagonian populations assigned to *M. venezuelensis* and *M. olmonae*, respectively (Barrio-Amorós et al. 2006;

Manzanilla et al. 2007, 2009). It is important, therefore, especially for a species classified as Endangered, to be certain that the same species occurs in all three areas.

Kenny (1969) reported the distribution of *F. fitzgeraldi* (then known as a member of the genus *Nototheca*) from surveys made during 1955–1961. He listed the frog as occurring “throughout Trinidad from sea level to the highest peaks,” and listed several locations in the Northern Range (including the summit of El Tucuche, Trinidad’s second highest mountain, the Aripo Valley, the mouth of Grande Riviere river, and Matelot); other locations were Rio Claro, Mayaro, and Tamana Hill. Later, Clarke et al. (1995) confirmed the presence of *F. fitzgeraldi* in two species of bromeliads on the summit of El Tucuche, but did not find it on Cerro del Aripo. Murphy (1997) added the Arima Valley, the road to Arena Dam, and Morne Bleu Ridge to the list of Trinidad records. He also listed Tobago locations at Northside Road, Hillsborough Dam, Speyside, and the Windward Road by Lambeau Crown Trace. The distribution map accompanying the IUCN Red List assessment (La Marca et al. 2004) shows *F. fitzgeraldi* occupying an area of 4,500 km² in all. This included areas in northeastern Venezuela, adjacent to Trinidad, of approximately 3,700 km²; an area of Trinidad, mainly in the central part of the Northern Range but extending a little south, of about 600 km²; and most of the northeast of Tobago, centered on the Main Ridge forest, of about 200 km². *A Field Guide to the Amphibians and Reptiles of Trinidad and Tobago* (Murphy et al. 2018) gives a similar picture for Tobago, but extends the Trinidad distribution somewhat to the west, east, and south, based on museum specimens and published records.

The aims of this paper are three-fold: a) to test whether the three populations of *F. fitzgeraldi* can safely be assigned to a single species using molecular methods; b) to collate recent data on the distribution and population size of *F. fitzgeraldi*, some published and some new in this paper, and c) to assess whether this species indeed qualifies for its current Endangered (EN) status.

Materials and Methods

Flectonotus fitzgeraldi specimens were collected at locations in Trinidad and Tobago, and Venezuela, under licenses from the Trinidad and Tobago Government Wildlife Section: Special Game Licenses issued for scientific purposes in 2012–2019 to John Murphy, Mike Rutherford, and Rick Lehtinen; and in Venezuela under the collection permit numbers 1375 and 0878 granted to Gilson A. Rivas by the República Bolivariana de Venezuela’s Ministerio del Poder Popular para

Ecosocialismo y Aguas. Voucher specimens are deposited in the Museo de Biología, Universidad del Zulia, Maracaibo (MBLUZ); Museo de la Estación Biológica de Rancho Grande, El Limón (EBRG), Museo de Historia Natural La Salle, Caracas (MHNLS), Rick Lehtinen field number (RML), and Museum of Zoology, University of West Indies (UWIZM). Animals used for genetic analysis were euthanized following the ASIH guidelines using MS-222 in water.

DNA Analysis

Adults and tadpoles of *Flectonotus fitzgeraldi* were caught with hand nets. The DNA was sequenced from 11 tadpole tail tips and adults (Table 1). Whole genomic DNA was extracted using the DNeasy Blood and Tissue kit (QIAGEN, Hilden, Germany) following the manufacturer's instructions. One mitochondrial gene fragment, 16S rDNA, was used with primers 16SL and 16SH (Palumbi 1991) and the 16S primers reported by Wiens et al. (2005). Templates were sequenced on both strands, and the complementary reads were used to resolve rare, ambiguous base-calls in Sequencher v4.9 (Gene Codes Corporation, Ann Arbor, Michigan, USA). The lengths of the sequences were not the same for all individuals as different primers were used in different laboratories. All *Flectonotus* 16S rDNA sequences were downloaded from GenBank ($n = 5$), but the final alignment included only four of them as the only Brazilian specimen (*Flectonotus* sp.) showed very high divergence from all other species. The total dataset consisted of 15 individuals, including two individuals of *Flectonotus pygmaeus* from Venezuela which were used as an outgroup. Sequences were aligned in Seaview v4.2.11 (Gouy et al. 2010) under ClustalW2 (Larkin et al. 2007) with default settings. The final alignment comprised 859 base pairs.

The most appropriate substitution model (TrN) was determined by the Bayesian Information Criterion (BIC) in jModeltest 2 (Posada 2008). Phylogenetic analyses were run to assess the relationships between localities, and taxa were inferred using the Bayesian Inference (BI) optimality criterion under the best-fitting substitution model. MrBayes v3 (Ronquist and Huelsenbeck 2003) was used with default priors and Markov chain settings, and with random starting trees. Each run consisted of four chains of 10 million generations, sampled every 10,000 generations. Phylogenetic relationships were also estimated using a Maximum Likelihood (ML) approach, as implemented in the software RAxML v7.0.4 (Silvestro and Michalak 2012), under the GTR model. All analyses were performed using the CIPRES platform (Miller et al. 2010). A median-joining haplotype network (Bandelt et al. 1999) was constructed using Popart v1.7 (Leigh and Bryant 2015). Because of missing data in the original alignment, a shorter alignment (500 bp) was used for the network analysis.

Survey Methods

The temporal pattern of calling. To establish the temporal pattern of calling in *F. fitzgeraldi*, in June 2006 an undisturbed site in Trinidad's Northern Range was chosen where the species had previously been recorded (Morne Bleu Ridge, Arima Valley, 10°43'37"N; 61°18'21"W, elevation 730 m; Murphy 1997). Starting from the radio-transmitter station at the west end of the trail, 20 sequential 100 m transects were marked out eastwards, using colored tape tied to trees. Trained observers walked the trail in pairs a total of eight times from June to August, from late afternoon until 2000 h, listening for both *F. fitzgeraldi* and *Pristimantis urichi*. Each 100-m transect required about 9 min to survey. Frog calls judged to be made from within a distance of approximately 5 m on either side of the trail were recorded (the numbers of frogs per transect were used for population estimates, as noted below, and this survey was repeated in June – August 2007). Since these species both call as dispersed individuals rather than in multi-individual choruses, a slow walk is a reliable way to estimate the number of calling frogs. To ensure there was no temporal bias in recording along the 2-km trail, the start times of the 20 transects were randomized.

Presence/absence surveys. Trinidad and Tobago: The observers who contributed to this study learned the call of *F. fitzgeraldi* either by listening to recordings made by Morley Read (no date recorded) or by Paul Hoskisson, or by visiting a site where *F. fitzgeraldi* is common and listening to the call at dusk, while also scanning the vegetation to obtain a sighting of the frogs. The surveys reported here used the frog's call as an evidence of presence, since searching for the frogs more directly can cause disturbance and may interfere with calling. Frogs were sometimes seen when listening was accompanied by torch use, but sightings were not used as a main criterion for presence. Surveys generally began just as light was fading, at about 1820 h, and continued until about 1930 h, when the calling declined in frequency. Some surveys were made by road from a vehicle, stopping to listen for calls. In this case, stops were made whenever a stand of *Heliconia bihai* was seen close to the road edge, since this plant had a strong association with *F. fitzgeraldi*. However, in the absence of *H. bihai*, stops were made every few hundred meters, since the frog also occurs in bromeliads on trees. Other surveys reported here were a component of regional Bioblitzes (DITOS consortium 2017) organized by the Trinidad and Tobago Field Naturalists' Club and the University of the West Indies Zoology Museum (2012–2019), which aimed to record every species encountered in an area over a 24-hour period. Two of the authors (John Murphy and Renoir Auguste) coordinated the herpetology group during these surveys, which involved a small team of observers walking slowly along forest trails from dusk

Table 1. *Flectonotus fitzgeraldi* vouchers, localities, and GenBank accession numbers.

| Voucher | Locality | GenBank accession number |
|------------------|---|--------------------------|
| MBLUZ 0395 | Venezuela, Cerro Humo, Península de Paria | MT968884 |
| MBLUZ 0448 | Venezuela, Cerro Humo, Península de Paria | MT968885 |
| EBRG 7337 | Venezuela, Cerro La Cerbatana | MT968886 |
| EBGR 7346 | Venezuela, Cerro Campeare | MT968887 |
| UWIZM.2015.18.4 | Trinidad, Aripo Savanna | MT968892 |
| UWIZM.2019.36 | Trinidad, Tamana | MT968883 |
| RML0115 | Tobago, Forest Reserve | MT968888 |
| RML0116 | Tobago, Forest Reserve | MT968889 |
| RML0117 | Tobago, Forest Reserve | MT968890 |
| RML0118 | Tobago, Forest Reserve | MT968891 |
| UWIZM.2012.27.23 | Tobago, Charlotteville (Flagstaff hill) | MT968882 |

onwards, listening for any frog calls, including those of *F. fitzgeraldi*. Another approach was the use of transects, where the number of frogs heard calling was recorded along a fixed length of trail. In some cases, audio recordings were made. Locations were recorded using a hand-held GPS device.

Venezuela: Data were assembled from the published literature and a revision of Venezuelan museum specimens (see specimen collection information above and Specimens Examined, Appendix 1).

Maps recording presence/absence were created with QGIS v3.0.2 software (<https://www.qgis.org/en/site/>) in WGS84 datum, using as a base layer the Google Terrain Hybrid (Map data ©2020 Google) as a base map (obtained through the Web Mapping Service in QGIS). GPS coordinates were contributed by the authors (see Supplementary Fig. S1). The extents of occurrence for *F. fitzgeraldi* were calculated for Trinidad, Tobago, and Venezuela individually using QGIS (version 3.0.2, Girona). GPS coordinates where the species was present were used to create a minimum convex polygon around the outermost coordinates within the country using the QGIS minimum bounding geometry tool applied using convex hull as the selected geometry type. The convex polygons thus created were clipped to their respective country's shape file so that areas of the polygons which extended into the sea were excluded. The areas of the clipped polygons were subsequently calculated to provide the extent of occurrence of the species for Trinidad, Tobago, and Venezuela in km² (see Supplementary Fig. S1).

Population estimates. Population densities were estimated for *Flectonotus fitzgeraldi* along Trinidad's Morne Bleu Ridge in 2006 and 2007 using transects at dusk, as described above (temporal pattern of calling). The number of calling males along a 100-m transect which was 10 m wide (1,000 m²) was extrapolated to give the

density in frogs per hectare. The site was surveyed again in 2012, 2013, and 2014, using the same methodology, except that only the first 150 m of the trail were surveyed. No specific population estimates were made in Tobago or in Venezuela (see Table 2 and comments in **Discussion**).

Results

DNA analysis. All specimens from Venezuela (Paria Biota region) recovered the same haplotype, while the Trinidad and Tobago frogs recovered two and three haplotypes, respectively (Fig. 1). The phylogenetic analyses recovered a well-supported monophyletic clade of all *Flectonotus fitzgeraldi* with low genetic differentiation throughout the nominal species range, reflecting a low genetic variability throughout. Only the Venezuelan frogs were monophyletic.

The temporal pattern of calling. Figure 2 shows the temporal pattern of calling at Morne Bleu Ridge, Trinidad, for both *Flectonotus fitzgeraldi* and *Pristimantis urichi*. The figure shows clearly that while single *F. fitzgeraldi* individuals may occasionally call in the afternoon, almost all call activity is concentrated within a narrow time period between 1800 h and 1915 h. The pattern of *P. urichi* serves as a comparison to the dusk-centered calling pattern of *F. fitzgeraldi*, and to show that the short calling period of *F. fitzgeraldi* is not due to some external factor such as weather.

Presence/absence surveys. Presence/absence survey results are shown in Table 2 and Fig. 3. GPS locations are given in Supplementary Table S1. For Trinidad and Tobago, most of the results are derived from survey data published here for the first time, with a few data points drawing on recently published papers. In Trinidad, we only failed to find any *Flectonotus fitzgeraldi* in a few surveyed locations (mainly Icacos in the southwest, and

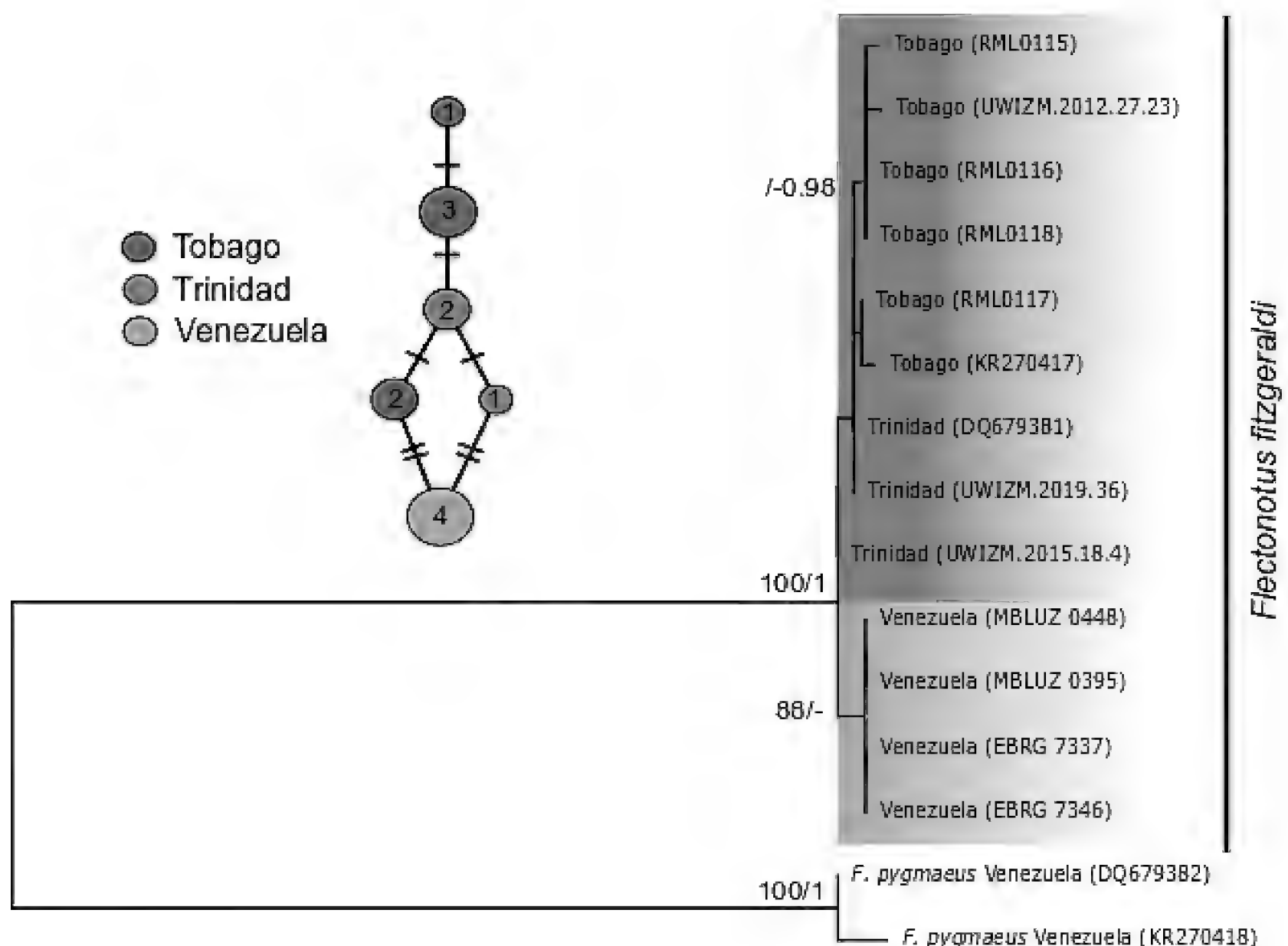


Fig. 1. Best Maximum Likelihood (ML) tree of *Flectonotus fitzgeraldi* populations from Trinidad, Tobago, and Venezuela. Values at the nodes are comprised of ML posterior probabilities (> 75%) and Bayesian Inference probabilities (> 95%). In the Medium-Joining network, numbers in circles represent the number of sequences with the same haplotype and dashes are number of substitutions.

the Port of Spain conurbation in the northwest). The largest areas remaining to be surveyed are in the southwest and south-central regions. In Tobago, the northeast has been surveyed extensively and *F. fitzgeraldi* has been found throughout. However, central Tobago is mountainous with few roads, and a large area remains unsurveyed. In Venezuela, systematic surveys were not conducted. Nevertheless, *F. fitzgeraldi* is reported as occurring throughout the Paria Peninsula and further west in northern Venezuela, including Cerros Campeare and La Cerbatana as well as the Turimiquire massif, as predicted by Rivas et al. (2018), and including sites from near sea level to 1,200 m asl. Most records from Venezuela come from disturbed locations within natural habitat areas, mainly along the edges of patches cleared for shifting agriculture or in gardens near paved roads. Our observations in the northeastern portion of the country were made at night; most frogs were detected visually, except six specimens that were heard calling at night (ca. 2000 h) in Campeare on 13 November 2016. Six specimens were observed staying on leaves of *Dracaena*, an ornamental plant (Asparagaceae),

during a survey that was carried out for visual inspection between 1700 and 2100 h. Specimens from La Cerbatana were observed resting inside the axil of a bromeliad, presumably *Tillandsia* sp. At Cerro Humo, individuals were observed on large leaves, possibly belonging to the aracean genus *Xanthosoma*.

Although these surveys were not intended to estimate population sizes, the number of calling males at any particular site was recorded in both Trinidad and Tobago in 2019. While the population of *F. fitzgeraldi* present was not quantified, the numbers of calling males were often considerable, especially in extensive stands of *Heliconia bihai*, with up to 35 being counted at Flagstaff Road in Tobago.

Population estimates. Population estimates for Morne Bleu Ridge, Trinidad, are shown in Table 3. The estimates are broadly similar across the years, except for 2006, which was the first year of these surveys, when the methodology was still being developed. The team leader for that year (JS) considers that the low average numbers resulted from the surveys starting too early in

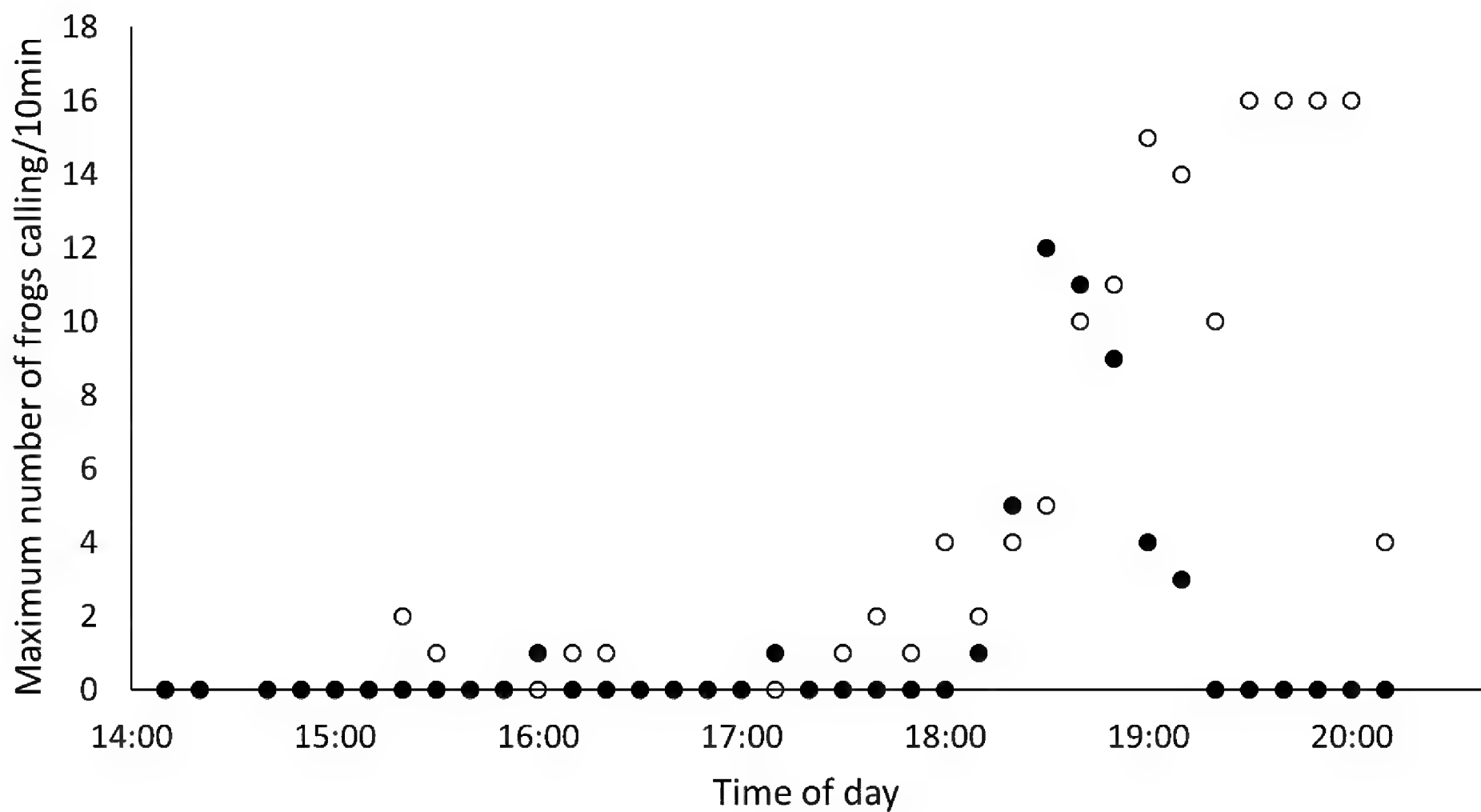


Fig. 2. Maximum numbers of frogs calling per 10 minutes during eight transects along the Morne Bleu ridge in 2006 (filled circles: *Flectonotus fitzgeraldi*; empty circles: *Pristimantis urichi*).

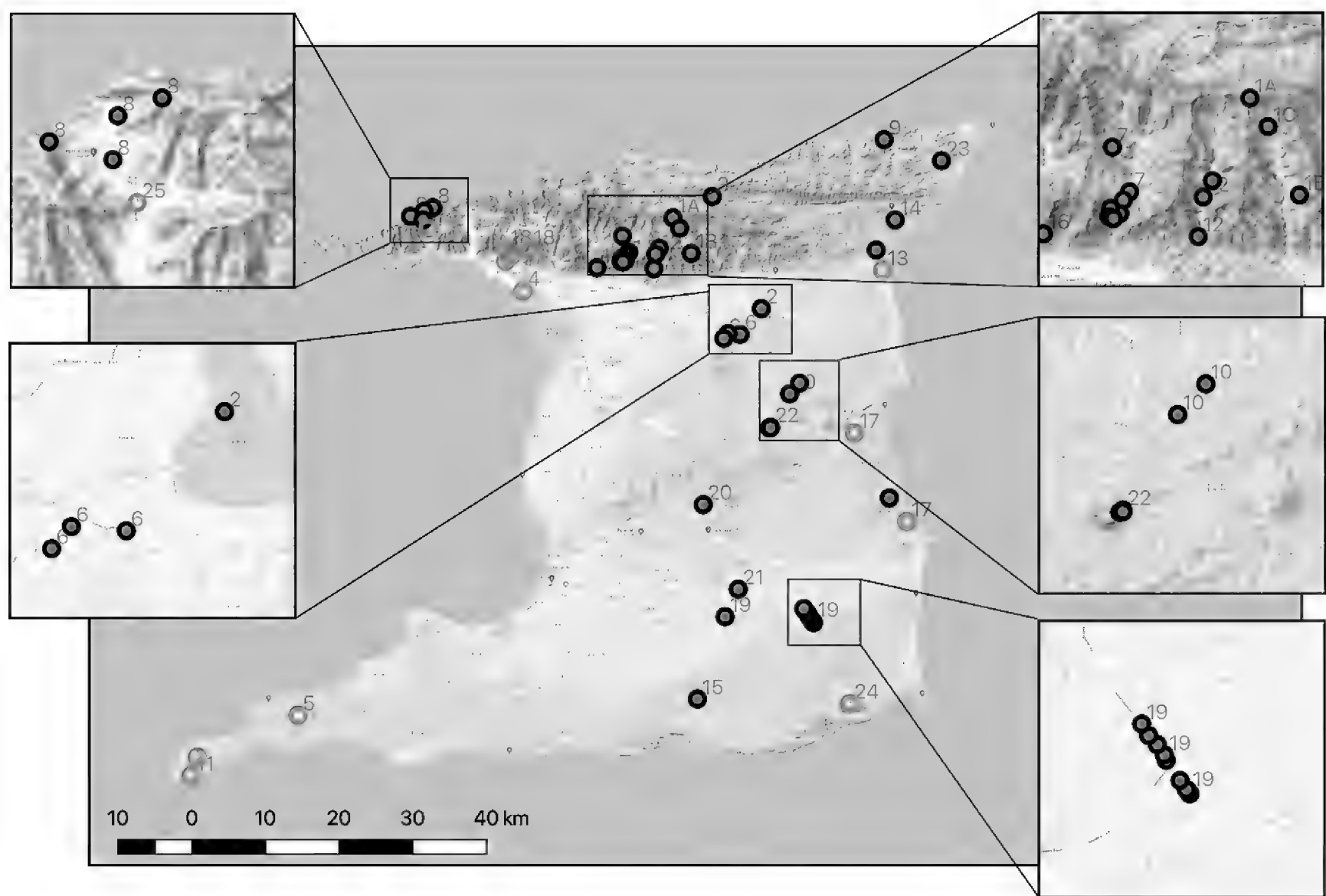


Fig. 3A. Map showing both presence and absence of *Flectonotus fitzgeraldi* as reported in this study in Trinidad. Location numbers correspond to those in Table 2.

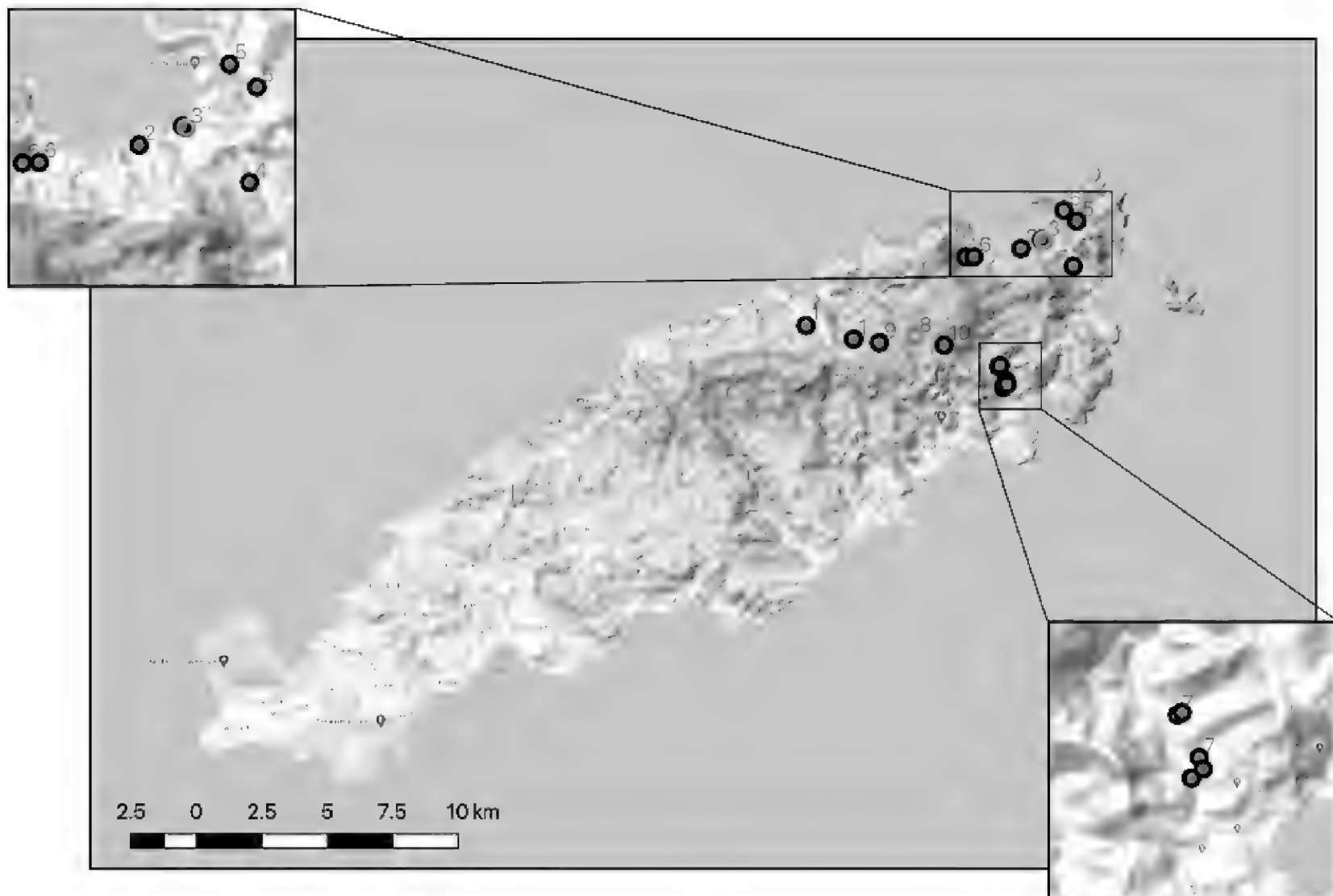


Fig. 3B. Map showing both presence and absence of *Flectonotus fitzgeraldi* as reported in this study in Tobago. Location numbers correspond to those in Table 2.

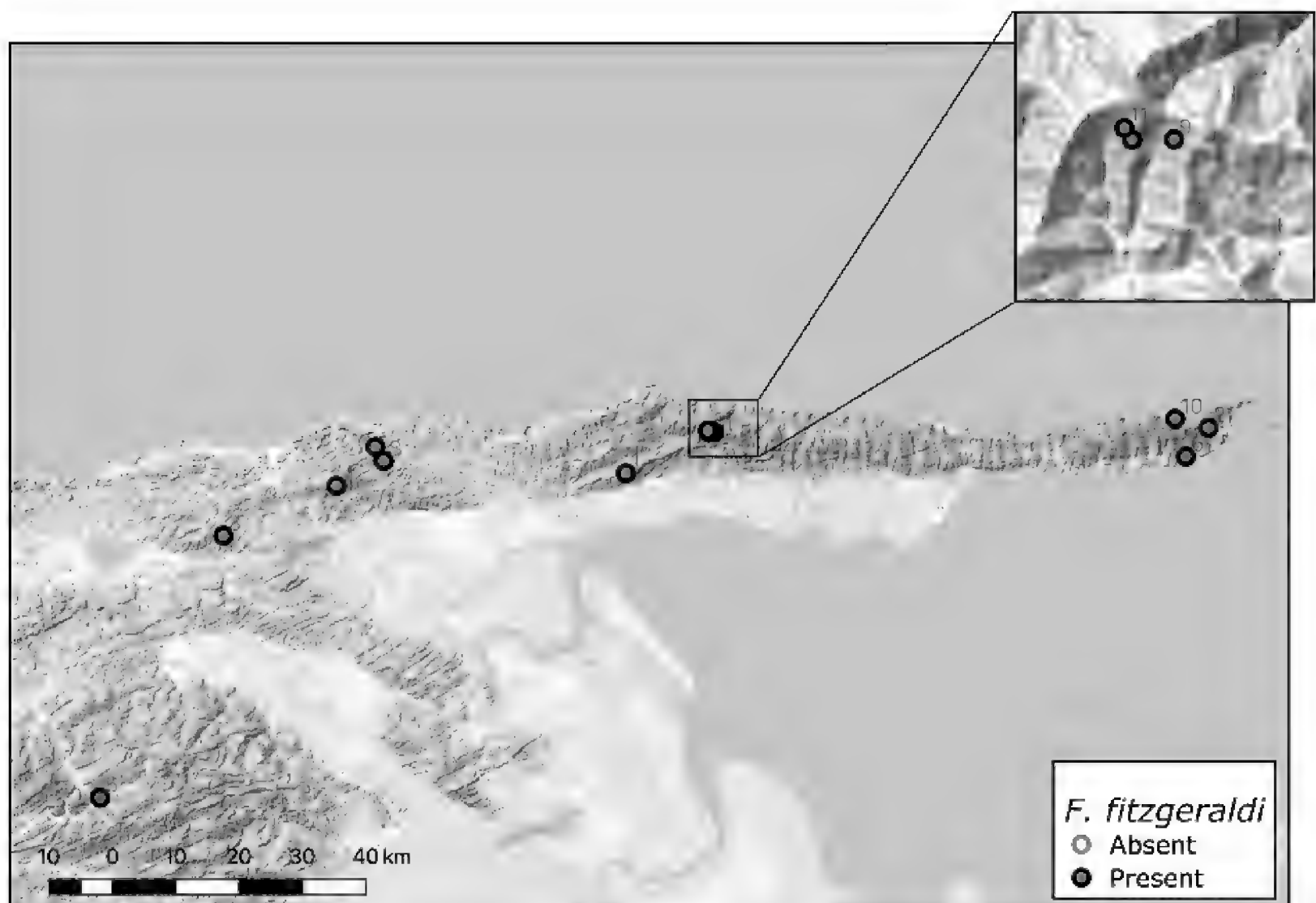


Fig. 3C. Map showing both presence and absence of *Flectonotus fitzgeraldi* as reported in this study in Venezuela. Location numbers correspond to those in Table 2.

Table 2. Results from presence/absence surveys for *Flectonotus fitzgeraldi* in A) Trinidad; B) Tobago, 2006–2019; and C) Venezuela. Numbers in parentheses following locations refer to numbers on the maps (Fig. 3). GPS co-ordinates for all locations are given in Supplementary Material 1. Superscripts in the “Year” column indicate sources of data: ¹Ogilvy et al. 2007; ²Smith 2008; ³Greener 2015; ⁴Bioblitz species lists (Rutherford 2013, 2014, 2017, 2018 a,b,c); ⁵Authors’ unpublished field notes; ⁶Auguste et al. 2015, Auguste and Hailey 2018; ⁷Auguste 2019; ⁸Mohammed et al. 2014; ⁹Eyre 2013; ¹⁰Rivas’ unpublished field notes; ¹¹Rivas et al. 2018; ¹²Barrio-Amorós et al. 2019; ¹³Duellman and Gray 1983; ¹⁴MBLUZ; ¹⁵EBRG; ¹⁶MHNL.

A) Trinidad

| Location | Year | Survey type | Findings on <i>F. fitzgeraldi</i> |
|------------------------------------|---|--------------------------------------|--|
| Arima Valley (1A): Morne Bleu | 2006 ¹ , 2007 ² , 2012 ³ , 2013 ^{3,4} , 2014 ³ , 2019 ⁵ | Audio path transects; Bioblitz | Always present at Morne Bleu ridge, Springhill Estate, Simla |
| (1B): Simla | As above | | |
| (1C): Springhill Estate | 2006 ¹ , 2007 ² | | |
| Aripo Savanna (2) | 2015 ⁶ | Audio and visual path transects | Abundant in marsh forest, but absent from savanna. Voucher collected 2015 |
| Brasso Seco (3) | 2019 ⁵ | Audio path transects | Present |
| Caroni Swamp, northern section (4) | 2016 ⁴ | Bioblitz | Absent |
| Chatham (5) | 2019 ⁵ | Audio transects | Absent |
| Cumuto-St. Raphael Road (6) | 2019 ⁵ | Audio road transect | Present wherever <i>Heliconia bihai</i> occurred (common) and in large bromeliads on trees, Arena Forest entrance |
| Caura Valley (7) | 2012 ³ , 2013 ³ , 2014 ³ , 2019 ⁵ | Audio transects | Present at two roadside sites, both before village; seven other locations |
| Edith Falls (8) | 2019 ⁵ | Audio path transects | Present; four locations |
| Grand Riviere (9) | 2019 ⁵ | Audio path transects | Present |
| Guaico-Tamana Road (10) | 2019 ⁵ | Audio road transect | Present at several sites between Cunaripo and Nestor, and along track to Tamana Hill, wherever <i>H. bihai</i> present |
| Icacos (11) | 2017 ⁴ , 2019 ⁵ | Bioblitz; audio road transects | Absent: forest trails by Grand lagoon; Southern Main Road |
| Lopinot Valley (12) | 2019 ⁵ | Audio road transects | Present; three locations |
| Matura Beach Road (13) | 2019 ⁵ | Audio road transect | Absent |
| Matura Forest (14) | 2016 ⁷ , 2019 ⁵ | Audio path transects | Present |
| Moruga (15) | 2019 ⁵ | Audio transects | Present |
| Mount St. Benedict (16) | 2012 ³ , 2013 ³ , 2014 ³ | Audio transects | Present |
| Nariva Swamp (17) | 2014 ⁴ , 2016 ⁷ | Bioblitz; audio and visual transects | Heard at Bush Bush, but not at Kernahan or Plum Mitán |
| Port of Spain (18) | 2016 ⁴ | Bioblitz | Absent at all sites checked (Botanics, St Ann’s, Mount Hololo, Lady Chancellor) |
| Rio Claro, roads south (19) | 2019 ⁵ | Audio road transect | Present; 12 locations |
| Tabaquite (20) | 2019 ⁴ | Bioblitz | Present |
| Tableland (21) | 2019 ⁵ | Audio transect | Present |
| Tamana Cave (22) | 2019 ⁵ | Audio and visual path transect | Present; three locations. Voucher collected 2019 |
| Toco (23) | 2018 ⁴ | Bioblitz | Present: Cumana forest trail |
| Trinity Hills (24) | 2014 ⁸ , 2016 ⁷ | Audio road transects | Heard at Edward Trace, 2014 but not in 2016 |
| Tucker valley (25) | 2012 ⁴ | Bioblitz | Absent |

B) Tobago

| Location | Year | Survey type | Findings on <i>F. fitzgeraldi</i> |
|------------------------------|---------------------------------------|--|---|
| Bloody Bay stream (1) | 2012 ⁹ , 2019 ⁵ | Daytime plant searches; audio path transects | Present in <i>Xanthosoma</i> ; heard from <i>H. bihai</i> away from stream |
| Cambleton (2) | 2019 ⁵ | Audio and visual transects | Abundant in <i>H. bihai</i> all along trail; absent from bamboo |
| Charlotteville (3) | 2015 ⁴ , 2019 ⁵ | Bioblitz; audio transects | None heard or seen along various forest trails, 2015, 2019. |
| Doctor's river (4) | 2019 ⁵ | Audio and visual transects | Seen and heard among <i>H. bihai</i> , three visits |
| Flagstaff hill (5) | 2012 ⁵ , 2019 ⁵ | Audio road transects | Abundant in roadside <i>H. bihai</i> stands; absent from bamboo. Voucher collected 2012 |
| Hermitage river (6) | 2019 ⁵ | Audio and visual transects | Abundant in <i>H. bihai</i> , not overhanging the stream, three visits |
| Louis D'Or streams (7) | 2019 ⁵ | Audio and visual transects | Present among <i>H. bihai</i> mainly, two visits |
| Main Ridge, Spring trail (8) | 2019 ⁵ | Audio and visual transects | Absent; few <i>H. bihai</i> in this dark closed canopy site; two visits |
| Main Ridge, Gilpin trail (9) | 2019 ⁵ | Audio path transects | Heard among streamside <i>H. bihai</i> |
| Main Ridge, central (10) | 2010 ⁵ , 2012 ⁹ | Daytime plant searches; audio path transects | Present in <i>Xanthosoma</i> ; heard among streamside <i>H. bihai</i> . Vouchers collected 2010 |

C) Venezuela

| Location | Year | Survey type | Findings on <i>F. fitzgeraldi</i> |
|---------------------------------------|-----------------------------|---------------------|--|
| Cachipal (1) | 2017 ^{10,14} | Visual transects | Present; vouchers collected |
| Camino desde Macuro-a Los Chorros (2) | 2003 ¹⁶ | Visual transects | Present: vouchers collected |
| Cerro Campeare (3) | 2016 ^{10,11,15} | Specimen collection | Several seen calling from <i>Dracaena</i> plants |
| Cerro La Cerbatana (4) | 2016 ^{11,15} | Visual transect | Present: vouchers collected |
| La Margarita (5) | 2013 ¹⁵ | Specimen collection | Present; vouchers collected |
| Macuro (6) | 2013 ¹² | Specimen observed | Present: photographed |
| Mauraco (7) | 1978 ^{13,15} | Specimen collection | Present: vouchers collected |
| Marauquito (8) | 1978 ¹⁶ | Specimen collection | Present: vouchers collected |
| Quebrada Las Melenas (9) | 2002, 2003 ^{11,16} | Visual transects | Present |
| Uquire (10) | 1993 ¹⁵ | Specimen collection | Present: vouchers collected |
| Cerro Humo (11) | 2015 ^{10,14} | Visual transect | Present: vouchers collected |

Table 3. Number of calling males of *Flectonotus fitzgeraldi* recorded at Morne Bleu Ridge, Trinidad. Data represent means based on eight surveys in 2006 and 2007; and five surveys in 2012–2014.

| Year | Mean (\pm SE) | Maximum |
|------|------------------|---------|
| 2006 | 19.5 \pm 4.7 | 80 |
| 2007 | 44 \pm 35.1 | 105 |
| 2012 | 51 \pm 15 | 80 |
| 2013 | 49 \pm 29 | 94 |
| 2014 | 64 \pm 27 | 94 |

the evenings, before the calling pattern had been fully determined. Mean as well as maximum numbers are shown. These numbers are for calling males only, so they must be considerable underestimates of the actual populations. Taken together, the mean and maximum numbers suggest that no significant change has occurred over the nine-year span of these surveys.

Extent of occurrence. Maps showing the extent of occurrence in each country are shown in Supplementary Fig. S1. The areas of occurrence are Trinidad: 2,922.4 km²; Tobago: 30.1 km²; and Venezuela: 3,713.4 km², yielding an overall total of 6,665.9 km².

Discussion

In cases where a species is widely distributed, and especially when its range is disjunct, it is important to assess whether significant intraspecific variation occurs. Duellman and Gray (1983) reported no significant morphological differences between the three respective populations of *Flectonotus fitzgeraldi* from Trinidad, Tobago, and Venezuela. The data here show highly similar genetic divergence between populations, while the Trinidad and Tobago animals were more closely related between them than to those from Venezuela. The lack of shared haplotypes suggests some degree of genetic isolation among all three localities.

La Marca et al. (2004) assessed the conservation status of *F. fitzgeraldi* as Endangered, on grounds of its area of occurrence being less than 5,000 km², its distribution being severely fragmented, and continuing declines in the extent and quality of its habitat. However, this assessment was not based on any published research. In order to obtain field data, it was necessary to establish an optimized survey methodology. These frogs call from the leaves of host plants, which encompass phytotelmata (bromeliads, *Heliconia*). Audio surveys at the time just following sunset are the best survey method for establishing presence or absence, either by walking, or by the use of a frequently stopping vehicle which can cover a longer distance at the critical time. With this method, we confirmed the frog's presence in the forests of the northeastern half of Tobago, and found it to occur wherever the host plants are common. In Trinidad, we greatly increased the frog's known occurrence to include the whole of the Northern Range mountains and the full length of the eastern half of the island; however, more surveys are needed to establish its extent in southwestern Trinidad. Our surveys in Venezuela have been less extensive, but the frog's presence was established further west and south than previously recorded. The total combined area of occurrence in the three countries is 6,665.9 km².

The assessment of frog population size in the tropics is highly problematic. Species such as *F. fitzgeraldi* are widely distributed and may call throughout the year

(Kenny 1969); they do not congregate to breed over a short time at a few established ponds. Only males call, and not necessarily every night. Greener et al. (2017) found that day-time visual sampling of the Trinidad stream frog underestimated the actual population (as established by removal sampling) by a factor of about three. Similarly, Lehtinen et al. (2016) showed, using new methods, that the Tobago stream frog, *Mannophryne olmonae*, is more abundant and widespread than previously considered. Our population estimates for *F. fitzgeraldi* should not, therefore, be regarded as true measures of the adult male population, let alone the total numbers of all classes of these frogs. However, we do think that our numbers could be valuable in assessing trends, when compared with future surveys using similar methods in the same locations. The data from Trinidad's Morne Bleu Ridge should be particularly useful in the future for assessing changes in a relatively undisturbed site.

In Venezuela, habitat loss in the Paria Peninsula is not a new issue (Kaiser et al. 2015), having been documented as early as the beginning of the 1940s. Beard (1945) found that local people were responsible for habitat disturbance mainly in the southern versant of the mountains, and that human density appeared to be too low to be in accordance with the vast area already deforested at that time. A similar case occurs in La Cibatana, where a continued deforestation occurs below 500 m (maximum altitude 1,000 m), but to a lesser degree than in Campearé, where natural vegetation only remains on the summits of the mountains (ca. 950 m). Finally, the natural forest formations present in the Turimiquire range are subject to some strong threats, as observed during a visit to the southeast side of the massif in 2006. The mountain area between 300 m and 1,200 m is severely affected by human activities. Pristine forests have been lost while the landscape has shifted to agricultural spaces and areas for human settlements. Land is mainly used to cultivate tomato and coffee, and to a lesser extent for livestock. Deforestation and cattle grazing have caused erosion and loss of nutrients in the soils. Additionally, these activities have encouraged the excessive use of agrochemicals, mostly monophosphates, affecting the mountain water bodies. Recently, however, most of these crops appear abandoned. Tate (1935) mentioned that the high elevations of Turimiquire did not escape deterioration, and noticed important areas devoted to coffee crops near 2,000 m elevation in the massif.

In conclusion, La Marca et al. (2004) estimated the total extent of occurrence of *F. fitzgeraldi* to be less than 5,000 km² and assessed its population to be declining. The low extent of occurrence, distribution in three separate countries, and declines in extent and quality of habitat led to a status assessment of Endangered. We show here that the species' extent of occurrence is well over 6,000 km² (Supplementary Fig. S1), that there is no evidence of population decline where we have been able to measure it (Trinidad), and that the extent and quality

of habitat in two countries (Trinidad and Tobago) show no signs of decline. However, because there are threats to habitat in the country with the largest area inhabited by the species (Venezuela), it is probably best to regard *F. fitzgeraldi* as Vulnerable.

Acknowledgements.—For allowing us to examine specimens under his care, we are grateful to Edward Camargo (EBRG). Gilson Rivas thanks Luis Sibira for his valuable help in the field, and A.L. Vilorio and J.M. González for their comments. Funding to work in Paria, Venezuela, has been generously provided by The Biodiversity Consultancy (Cambridge, United Kingdom) through Oro Verde (Bonn, Germany) to Gilson Rivas and Mayke De Freitas. Fieldwork in Trinidad and Tobago by staff and students of the Universities of Glasgow, Edinburgh, and Strathclyde was supported by small grants from many institutions including the Universities, the Glasgow Natural History Society, Dennis Curry's Charitable Trust, the Thriplow Trust, and the Gilchrist Educational Trust. We thank all the students who helped with the fieldwork. We also thank the members of the Trinidad and Tobago Field Naturalists' Club who contributed observations to the annual Bioblitzes from which we have drawn some of the data reported here. Rick Lehtinen acknowledges the Tobago House of Assembly for issuing research permits and the College of Wooster (Wooster, Ohio, USA) for funding. We also thank two reviewers (S. Lotzkat, H. Kaiser) for making suggestions which allowed us to improve this paper.

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Appendix 1. Specimens examined.

Flectonotus fitzgeraldi. VENEZUELA: Monagas: La Margarita, Turimiquire, 1,200 m, 10°10'32"N, 63°30'24"W (EBRG 7034-35). Sucre: Mauraco, N del Pilar, 10°40'17.62"N, 63°06'38.64"W (EBRG 519-520). Marauquito, Península de Paria, 400 m, (MHNLS 10859). Vertiente Sur de Cerro Humo, Península de Paria, 800 m, 10°42' N, 62°37' W (MBLUZ 0395, 0448). Alrededores de las Melenas, Península de Paria, 10°41'32.1"N, 62°37'24.9"W (MHNLS 15741, 16187). Camino desde Macuro a los Chorros, Península de Paria, 500 m, 10°41'54"N, 61°54'45"W (MHNLS 16199-17201). Uquire, vertiente Norte de la Península de Paria, 150 m, 10°43'N, 63°58' W (EBRG 2585). Cachipal, Península de Paria, 10°38'02.5"N, 62°45'01.8"W (MBLUZ 447). Cerro La Cerbatana, ~800 m, 10°37' N -63°10' W (EBRG 7336–7337). Cerro Campeare, 800 m, 10°32'45.4"N, 63°19'45.6"W (EBRG 7343–7346). Macuro, Península de Paria (photographed in Barrio-Amorós et al. 2019: 54).



Jo Smith is a general zoology enthusiast, who accidentally ended up studying and falling in love with treefrogs over the course of her Ph.D. on adhesion in the Hylidae, which involved many enjoyable years going back and forth to Trinidad from Glasgow on field work. She is now a Senior Lecturer at the Bangor University, Wales, where she tries her best to remind their very keen zoology with herpetology students that snakes are not the only herps.



Michael J. Jowers is an evolutionary biologist with broad interests in the processes and the timings of speciation. His work focuses on tropical island biogeography, phylogeography, systematics, population genetics, taxonomy, and conservation. Michael is deeply involved in amphibian and reptile studies from the islands of Trinidad and Tobago (Lesser Antilles), but he is also interested in other organisms such as birds, mammals, and insects. He actively leads studies throughout South America, Africa, Europe, and Asia.



Renoir J. Auguste is a Trinidad and Tobago herpetologist. Renoir received his M.Sc. in Biodiversity Conservation from The University of the West Indies, St. Augustine Campus, Trinidad and Tobago, and is interested in the ecology and conservation of amphibians and reptiles. He has conducted herpetological surveys across Trinidad and Tobago for national baseline surveys aimed at improving protected areas, as part of his academic degrees. He also volunteers with the local environmental NGO Trinidad and Tobago Field Naturalists' Club, in which he has held the position of President for three years.



Paul A. Hoskisson is Professor of Molecular Microbiology at the Strathclyde Institute of Pharmacy and Biomedical Sciences (Scotland) and the Royal Academy of Engineering Research Chair in Engineering Biology. While his research is primarily focused on the biosynthesis of antibiotics, but he also maintains research interests in amphibian reproduction, behavior, and conservation. Paul is a member of Royal Society of Biology Council.



Cammy Beyts is a Ph.D. student in Behavioral Ecology at The University of Edinburgh, Scotland, within the Institute of Evolutionary Biology. Cammy's research investigates the effects of local adaption and the development environment on inter-individual differences in tadpole behavior in species such as *Engystomops pustulosus* and *Leptodactylus fuscus*. Cammy has been conducting her fieldwork in Trinidad since 2018, and regularly assists with additional projects on a variety of herpetofauna while there.



Greig McInnes Muir is a recent Zoology graduate from the University of Edinburgh, Scotland. Greig cultivated a passion for herpetology during his undergraduate research project on the repeatable inter-individual differences in behavior of the model species *Engystomops pustulosus*, while on expedition to Trinidad. Currently working within the pharmaceutical industry, Greig is still a keen naturalist and is always looking for ways to keep connected to nature, conservation, and behavioral ecology.



Mark Steven Greener developed an interest in amphibians and reptiles at a young age. He further cultivated this passion at the University of Glasgow, Scotland, where he participated in and led several scientific expeditions. Following this, Mark moved to the Wildlife Health Ghent lab group at the University of Ghent, Belgium, pursuing a Ph.D. on the dynamics of chytrid fungus in Northern Europe. He has been a part of multiple projects and has published several papers on the amphibians and other wildlife of Trinidad.



Daniel G. Thornham is a zoologist and entomologist at the School of Natural Sciences, Bangor University, North Wales, looking at relationships in phytotelm ecology, biomechanics, and proximate behavioral ecology. Using pitcher plants (Nepenthaceae) and bromeliads (Bromeliaceae) as model ecological systems, Dan explores the specializations of animals living in the aerial aquatic habitats formed by these plants. In Bangor, Dan teaches undergraduate research skills, invertebrate biology, and field techniques modules, and holds a number of academic roles in the School. He has been visiting Trinidad periodically since 2000 and loves nothing more than eating doubles after a long climb into the canopy to explore the bromeliads.



Isabel Byrne is an Irish researcher who received a B.Sc. in Zoology from the University of Glasgow, Scotland. Her previous research focused on the herpetofauna of the rainforests and coast of the North East of Tobago, with special interest in the Tobago Glass Frog, *Hyalinobatrachium orientale tobagoense*. In 2020, she completed an M.Sc. in *One Health: Humans, Animals, and the Environment*, at the Royal Veterinary College and the London School of Hygiene and Tropical Medicine in England. She is currently working as a research assistant at the London School of Hygiene and Tropical Medicine on the analysis of spatial and environmental data related to malaria vector abundance, and epidemiological risk analysis.



Richard (“Rick”) Lehtinen has studied the ecology, evolution, behavior, and conservation of amphibians and reptiles for 25 years. He has authored or co-authored over 50 books, monographs, and research articles on amphibians and reptiles with primary interests in the specializations of plant-breeding frogs, the evolution of parental care behavior, and the long-term study of population dynamics. Primarily a field biologist, Rick has enjoyed probing the secrets of nature in Costa Rica, Madagascar, Taiwan, Trinidad and Tobago, and the United States. He holds a Ph.D. from the University of Michigan and is currently Professor of Biology at the College of Wooster (Ohio, USA).



Meredith Eyre worked as a student in Dr. Lehtinen’s group at the College of Wooster (Ohio, USA), and under his guidance, her senior thesis explored the natural history and habitat selection of *Flectonotus fitzgeraldi* in Tobago. She continues to be inspired by the research opportunities created for her at the undergraduate level, and after completing her M.S. at the Ohio State University, she has dedicated herself to the development of similarly empowering opportunities for others. She currently serves as a Laboratory Instructor at Carlow University (Pennsylvania, USA), where she delights in working primarily with introductory-level students as they begin their journey into the field of biology.



Michael G. Rutherford is a naturalist based in Scotland. A lifelong interest in animals led him to a degree in Zoology from Glasgow University, Scotland, followed by a masters in conservation biology at James Cook University, Australia. His jobs have included research assistant studying skinks in Queensland, tropical house zookeeper for Newquay Zoo (England), curator of invertebrates for Glasgow Museums (Scotland) and curator of the University of the West Indies Zoology Museum in Trinidad and Tobago. His research interests include reptiles, land snails, millipedes, oilbirds, and biological recording.



John C. Murphy is a naturalist with a focus on snakes. When he is not hiking in the desert or examining specimens in the lab, he is often writing about reptiles. Murphy is a retired science educator who got serious about his lifelong fascination with lizards and snakes in the early 1980s when he and his family made their first trip to Trinidad. The work on Trinidad and Tobago provided valuable lessons that shaped his views of nature and evolution, and today he is still working on the eastern Caribbean herpetofauna. In the 1990s, he did some work on homalopsid snakes in Southeast Asia with others from the Field Museum (Chicago, Illinois, USA). He now resides in southeastern Arizona and is involved in multiple projects on arid habitats and the impacts of climate change on biodiversity. His most recent book is *Giant Snakes, a Natural History* (with co-author Tom Crutchfield). Born and raised in Joliet, Illinois, he first learned about reptiles on his grandfather’s farm by watching Eastern Garter Snakes emerge from their winter dens and Snapping Turtles depositing their eggs at the edge of a cattail marsh.



Mayke De Freitas Santos is a conservationist with postgraduate studies in International Environmental Law (SOAS) and Conservation Leadership (University of Cambridge, England) who has worked for various international NGOs both in Venezuela and Europe. Mayke focuses on the governance of protected areas, as well as remote sensing and habitat quality assessments of amphibian species. He is a contributor to the IUCN Red List for several species of amphibians and reptiles from the Peninsula de Paria, Venezuela, where he has worked since 2011.



Gilson A. Rivas was born in Caracas, Venezuela. He currently serves as co-editor of the scientific journal *Anartia*, and is a collection manager at the Museo de Biología de la Universidad del Zulia, Maracaibo—a Venezuelan centennial university that began academic activities on 11 September 1891. For over two decades, Gilson has been devoted to the taxonomy and conservation of the neotropical herpetofauna, having authored or co-authored more than 100 academic publications, and describing over 30 new species of amphibians and reptiles, and a new genus of dipsadine snake, *Plesiodipsas*. Gilson is the author (with G. Ugueto) of the book *Amphibians and Reptiles of Margarita, Coche, and Cubagua*; and together with M. De Freitas, H. Kaiser, C.L. Barrio-Amorós, and T.R. Barros produced *Amphibians of the Península de Paria: a Pocket Field Guide*. Gilson's research interests are focused on the herpetofauna of the Venezuelan coastal range and insular ecosystems, as well as the influences of invasive species and human development and their impact on the native fauna.



J. Roger Downie is a semi-retired Professor of Zoological Education at the University of Glasgow, Scotland. During his long association with Trinidad and Tobago, he has contributed to research on amphibians and marine turtles in collaboration with Glasgow students, and many others, on numerous research expeditions.

Supplementary Fig. S1 Maps showing the GPS coordinates where *Flectonotus fitzgeraldi* was found to be present and clipped polygon shapes used to calculate the total area of occurrence for *F. fitzgeraldi* in Trinidad, Tobago, and Venezuela (Supplementary Fig. S1a–c). The areas of occurrence are Trinidad: 2,922.4 km²; Tobago: 30.1 km²; and Venezuela: 3,713.4 km².

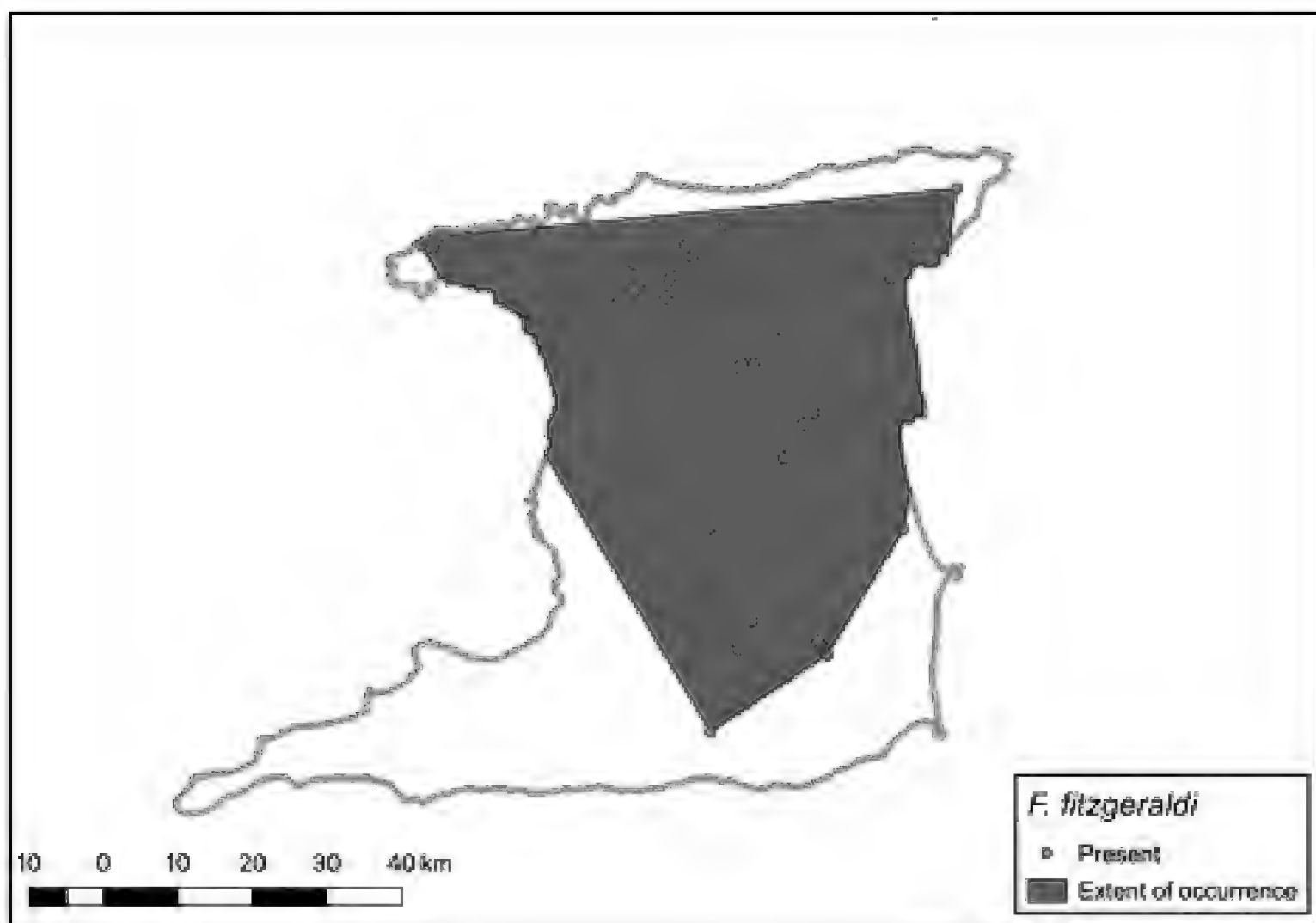


Fig. S1a. Presence and total area of *Flectonotus fitzgeraldi* occurrence in Trinidad.

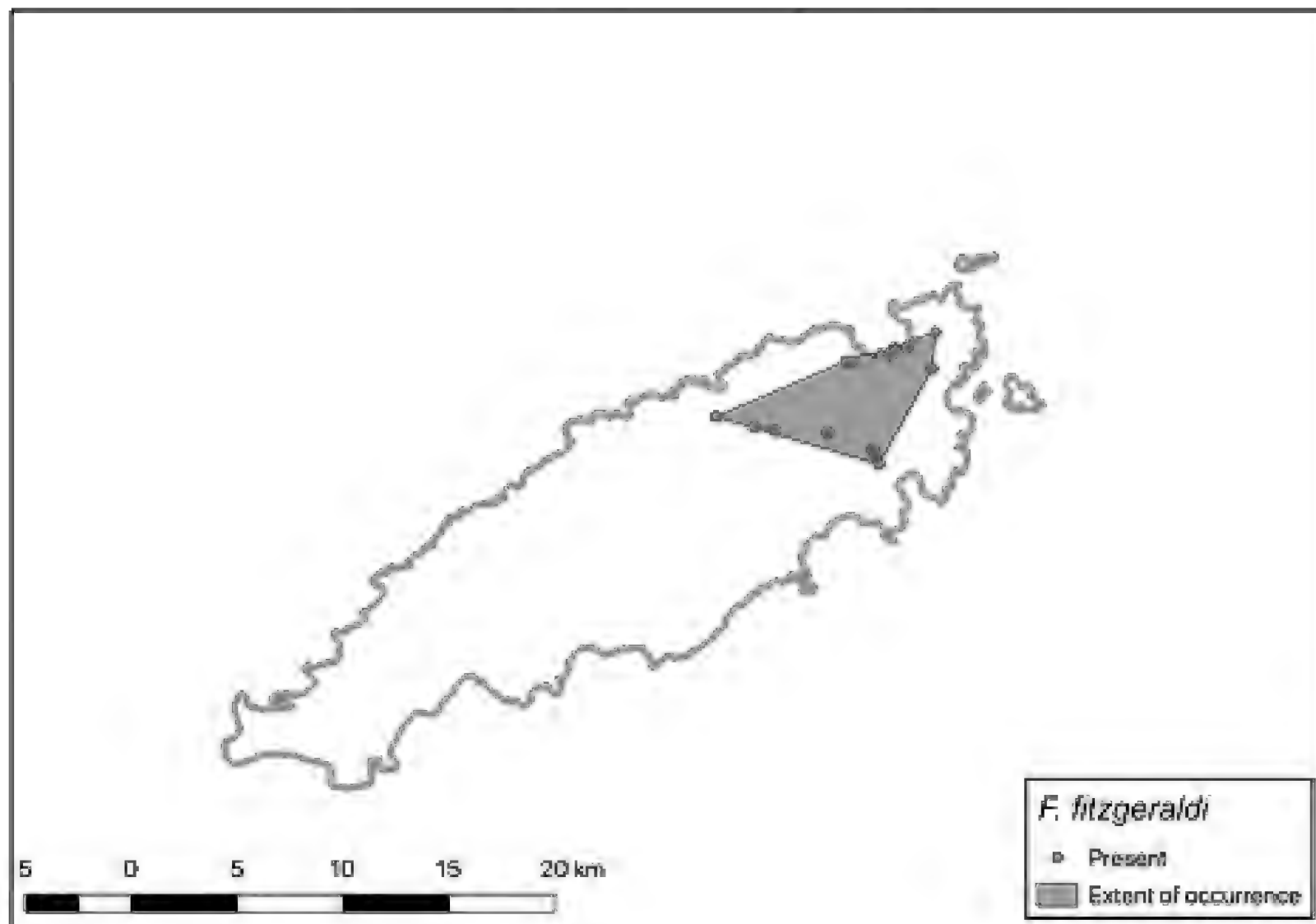


Fig. S1b. Presence and total area of *Flectonotus fitzgeraldi* occurrence in Tobago.

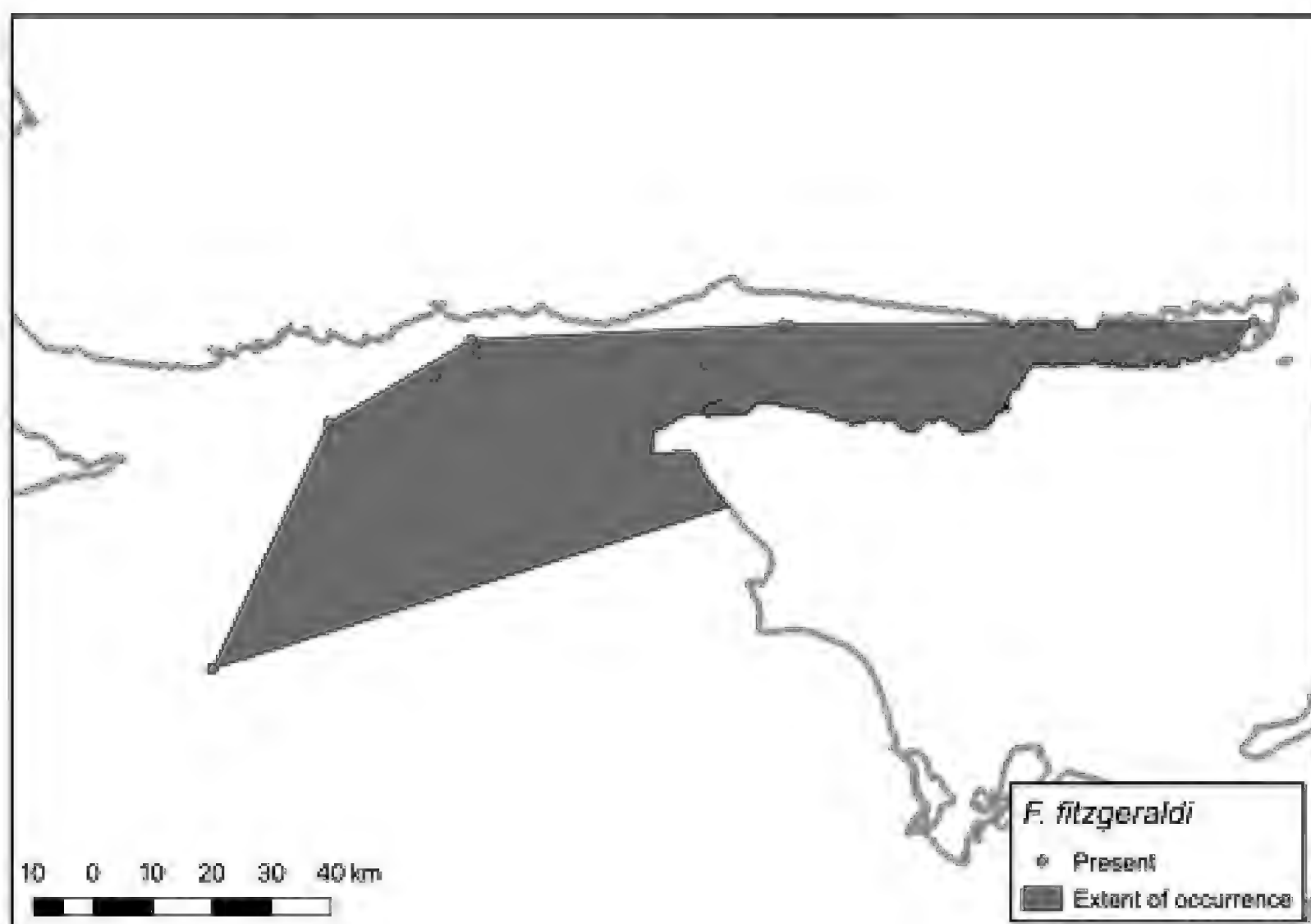


Fig. S1c. Presence and total area of *Flectonotus fitzgeraldi* occurrence in Venezuela.

Supplementary Table S1. Complete dataset of sites in Trinidad, Tobago, and Venezuela surveyed for *Flectonotus fitzgeraldi* in this study. The “Site no.” column refers to the numbered locations in Fig. 3 and Table 2.

| Year(s) | Country | Location | Site no. | Coordinates | Present / absent | Source |
|------------------------------------|----------|-----------------------------------|----------|----------------------------|------------------|---|
| 2019 | Tobago | Bloody Bay Stream | 1 | 11°17'26.5"N; 60°38'00.7"W | Present | Authors' unpub. field notes, 2019 |
| 2012 | Tobago | Bloody Bay Stream | 1 | 11°17'9.8"N; 60°37'00.9"W | Present | Eyre 2013 |
| 2019 | Tobago | Cambleton Trail | 2 | 11°19'01.5"N; 60°33'29.5"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Manowar Cottages (Charlotteville) | 3 | 11°19'12.6"N; 60°33'03.7"W | Present | Authors' unpub. field notes, 2019 |
| 2015 | Tobago | Manowar Cottages (Charlotteville) | 3 | 11°19'11.5"N; 60°33'01.5"W | Absent | Rutherford 2018a |
| 2019 | Tobago | Doctors River | 4 | 11°18'39.7"N; 60°32'23.7"W | Present | Authors' unpub. field notes, 2019 |
| 2012 | Tobago | Flagstaff Hill Charlotteville | 5 | 11°19'48.7"N; 60°32'35.5"W | Present | Authors' unpub. field notes, 2012 |
| 2019 | Tobago | Flagstaff Hill Windward Road | 5 | 11°19'35.4"N; 60°32'19.2"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Hermitage River | 6 | 11°18'51.0"N; 60°34'39.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Hermitage | 6 | 11°18'51.4"N; 60°34'29.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Louis D'Or Streams | 7 | 11°16'36.0"N; 60°33'58.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Louis D'Or Streams | 7 | 11°16'10.0"N; 60°33'52.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Louis D'Or Streams | 7 | 11°16'37.0"N; 60°33'56.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Louis Original | 7 | 11°16'18.5"N; 60°33'48.8"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Louis Second | 7 | 11°16'13.8"N; 60°33'47.2"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Main Ridge (Spring Trail) | 8 | 11°17'12.5"N; 60°35'43.9"W | Absent | Authors' unpub. field notes, 2019 |
| 2019 | Tobago | Main Ridge (Gilpin Trail) | 9 | 11°17'05.3"N; 60°36'28.4"W | Present | Authors' unpub. field notes, 2019 |
| 2010, 2012 | Tobago | Main Ridge (central) | 10 | 11°17'02.2"N; 60°35'06.8"W | Present | Authors' unpub. field notes, 2010, Eyre 2013 |
| 2006, 2007, 2012, 2013, 2014, 2019 | Trinidad | Morne Bleu (Arima Valley) | 1A | 10°43'37.0"N; 61°18'21.0"W | Present | Ogilvy et al. 2007; Smith 2008; Greener 2015; Rutherford 2014; Authors' field notes, 2019 |
| 2006, 2007, 2012, 2013, 2014, 2019 | Trinidad | Simla (Arima Valley) | 1B | 10°41'01.0"N; 61°16'59.9"W | Present | Ogilvy et al. 2007; Smith 2008; Greener 2015; Rutherford 2014; Authors' field notes, 2019 |
| 2006, 2007 | Trinidad | Springhill Estate (Arima Valley) | 1C | 10°42'51.1"N; 61°17'51.4"W | Present | Ogilvy et al. 2007; Smith 2008 |
| 2015 | Trinidad | Aripo Savanna | 2 | 10°36'59.0"N; 61°11'47.0"W | Present | Auguste et al. 2015; Auguste and Hailey 2018 |
| 2019 | Trinidad | Brasso Seco | 3 | 10°45'10.3"N; 61°15'26.0"W | Present | Authors' unpub. field notes, 2019 |
| 2016 | Trinidad | Caroni Swamp, Northern Section | 4 | 10°38'16.8"N; 61°29'29.8"W | Absent | Bioblitz, 2016 |
| 2019 | Trinidad | Chatham | 5 | 10°07'17.1"N; 61°46'11.8"W | Absent | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Cumuto St. Raphael Road | 6 | 10°35'06.0"N; 61°13'22.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Cumuto St. Raphael Road | 6 | 10°35'10.0"N; 61°14'15.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Cumuto St. Raphael Road | 6 | 10°34'49.0"N; 61°14'34.0"W | Present | Authors' unpub. field notes, 2019 |

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Supplementary Table S1 Continued. Complete dataset of sites in Trinidad, Tobago, and Venezuela surveyed for *Flectonotus fitzgeraldi* in this study. The “Site no.” column refers to the numbered locations in Fig. 3 and Table 2.

| Year(s) | Country | Location | Site no. | Coordinates | Present / absent | Source |
|------------------|----------|--|----------|----------------------------|------------------|-----------------------------------|
| 2012, 2013, 2014 | Trinidad | Caura Valley | 7 | 10°40'02.0"N; 61°22'08.0"W | Present | Greener 2015 |
| 2012, 2013, 2014 | Trinidad | Caura Valley | 7 | 10°40'27.1"N; 61°22'09.0"W | Present | Greener 2015 |
| 2019 | Trinidad | Caura Valley | 7 | 10°42'17.7"N; 61°22'06.1"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Caura Valley | 7 | 10°41'06.1"N; 61°21'38.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Caura Valley | 7 | 10°40'52.6"N; 61°21'48.3"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Caura Valley | 7 | 10°40'30.9"N; 61°21'54.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Caura Valley | 7 | 10°40'39.3"N; 61°22'08.9"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Caura Valley | 7 | 10°40'26.2"N; 61°22'11.9"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Caura Valley | 7 | 10°40'23.0"N; 61°22'04.3"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Edith Falls | 8 | 10°44'21.3"N; 61°36'50.2"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Edith Falls | 8 | 10°44'05.9"N; 61°36'50.8"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Edith Falls | 8 | 10°43'45.3"N; 61°37'04.1"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Edith Falls | 8 | 10°43'27.7"N; 61°36'54.5"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Grande Riviere | 9 | 10°49'19.0"N; 61°02'39.9"W | Present | Authors' unpub. field notes |
| 2019 | Trinidad | Guaico Tamana Rd. | 10 | 10°31'33.0"N; 61°08'57.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Guaico Tamana Rd. | 10 | 10°30'46.0"N; 61°09'41.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Icacos Southern Main Road | 11 | 10°04'13.7"N; 61°53'39.9"W | Absent | Authors' unpub. field notes |
| 2017 | Trinidad | Icacos | 11 | 10°02'51.4"N; 61°54'07.2"W | Absent | Rutherford 2018c |
| 2019 | Trinidad | Lopinot Valley | 12 | 10°41'23.9"N; 61°19'22.4"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Lopinot Valley | 12 | 10°40'57.8"N; 61°19'37.6"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Lopinot Valley | 12 | 10°39'54.0"N; 61°19'45.7"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Matura Beach Road | 13 | 10°39'46.8"N; 61°02'47.6"W | Absent | Authors' unpub. field notes |
| 2019 | Trinidad | Matura Forest | 14 | 10°41'16.0"N; 61°03'15.4"W | Present | Authors' unpub. field notes, 2019 |
| 2016 | Trinidad | Matura Forest | 14 | 10°43'27.8"N; 61°01'50.9"W | Present | Auguste et al. 2019 |
| 2019 | Trinidad | Moruga | 15 | 10°08'28.0"N; 61°16'32.2"W | Present | Authors' unpub. field notes, 2019 |
| 2012, 2013, 2014 | Trinidad | Mt. St. Benedict | 16 | 10°39'58.4"N; 61°23'59.1"W | Present | Greener 2015 |
| 2014 | Trinidad | Bush Bush Wildlife Sanctuary, Nariva Swamp | 17 | 10°23'09.6"N; 61°02'16.8"W | Present | Rutherford 2017 |

Supplementary Table S1 Continued. Complete dataset of sites in Trinidad, Tobago, and Venezuela surveyed for *Flectonotus fitzgeraldi* in this study. The “Site no.” column refers to the numbered locations in Fig. 3 and Table 2.

| Year(s) | Country | Location | Site no. | Coordinates | Present / absent | Source |
|---------|-----------|--|----------|----------------------------|------------------|--|
| 2016 | Trinidad | Plum Mitán, Nariva Swamp | 17 | 10°27'54.7"N; 61°04'52.3"W | Absent | Auguste et al. 2019 |
| 2016 | Trinidad | Kernahan, Nariva Swamp | 17 | 10°21'25.9"N; 61°00'59.0"W | Absent | Auguste et al. 2019 |
| 2016 | Trinidad | St. Ann's, Port of Spain | 18 | 10°40'52.3"N; 61°30'21.6"W | Absent | Rutherford 2018b |
| 2016 | Trinidad | Mt. Hololo, Port of Spain | 18 | 10°41'18.2"N; 61°29'03.8"W | Absent | Rutherford 2018b |
| 2016 | Trinidad | Botanic Gardens, Port of Spain | 18 | 10°40'26.4"N; 61°30'47.5"W | Absent | Rutherford 2018b |
| 2016 | Trinidad | Lady Chancellor, Port of Spain | 18 | 10°41'18.2"N; 61°30'47.5"W | Absent | Rutherford 2018b |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'03.5"N; 61°07'55.1"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'03.4"N; 61°07'55.4"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'05.9"N; 61°07'56.9"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'06.2"N; 61°07'57.6"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'07.0"N; 61°07'58.2"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'15.1"N; 61°08'04.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'29.1"N; 61°14'29.1"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'33.0"N; 61°08'16.3"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'37.5"N; 61°08'17.9"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'46.6"N; 61°08'24.2"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°14'54.6"N; 61°08'31.9"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Rio Claro, roads south | 19 | 10°15'04.8"N; 61°08'38.2"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Tabaquite | 20 | 10°22'40.8"N; 61°16'06.2"W | Present | Bioblitz, 2019 |
| 2019 | Trinidad | Tableland | 21 | 10°16'30.0"N; 61°13'30.0"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Tamana Caves | 22 | 10°28'16.2"N; 61°11'11.5"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Tamana Caves | 22 | 10°28'19.6"N; 61°11'06.5"W | Present | Authors' unpub. field notes, 2019 |
| 2019 | Trinidad | Tamana Caves | 22 | 10°28'17.0"N; 61°11'10.9"W | Present | Authors' unpub. field notes, 2019 |
| 2018 | Trinidad | Cumana Forest, Toco | 23 | 10°47'47.0"N; 60°58'23.5"W | Present | Bioblitz, 2018 |
| 2016 | Trinidad | Trinity Hills | 24 | 10°08'08.5"N; 61°05'13.2"W | Absent | Auguste et al. 2019 |
| 2014 | Trinidad | Trinity Hills | 24 | NA | Present | Mohamed et al. 2014 |
| 2012 | Trinidad | Tucker Valley | 25 | 10°42'50.4"N; 61°36'33.1"W | Absent | Rutherford 2013 |
| 2017 | Venezuela | Cachipal | 1 | 10°38'02.5"N; 62°45'01.8"W | Present | MBLUZ 447; Rivas' unpub. field notes, 2017 |
| 2003 | Venezuela | Camino desde Macuro a Los Chorro (vía Uquire) Península de Paría | 2 | 10°41'54.0"N; 61°54'45.0"W | Present | MHNLS 16199–16201 |

Supplementary Table S1 Continued. Complete dataset of sites in Trinidad, Tobago, and Venezuela surveyed for *Flectonotus fitzgeraldi* in this study. The “Site no.” column refers to the numbered locations in Fig. 3 and Table 2.

| Year(s) | Country | Location | Site no. | Coordinates | Present / absent | Source |
|------------|-----------|--------------------------------|----------|----------------------------|------------------|--|
| 2016 | Venezuela | Cerro Campeare | 3 | 10°32'45.4"N; 63°19'45.6"W | Present | Rivas' unpub. field notes, 2016; Rivas et al. 2018; EBRG |
| 2016 | Venezuela | Cerro La Cerbatana | 4 | 10°37'05.8"N; 63°10'45.3"W | Present | Rivas et al. 2018; EBRG |
| 2013 | Venezuela | La Margarita, Turimiquire | 5 | 10°10'32.0"N; 63°30'24.0"W | Present | EBRG 7034–35 |
| 2013 | Venezuela | Macuro, Península de Paria | 6 | 10°39'08.0"N; 61°56'11.0"W | Present | Barrio-Amorós et al. 2019 |
| 1978 | Venezuela | Mauraco, N del Pilar | 7 | 10°40'17.6"N; 63°06'38.6"W | Present | Duellman and Gray 1983; EBRG 519–520 |
| 1978 | Venezuela | Marauquito, Península de Paria | 8 | 10°39'06.0"N; 63°05'56.0"W | Present | MHNLS 10859 |
| 2002, 2003 | Venezuela | Quebrada Las Melenas | 9 | 10°41'32.1"N; 62°37'24.9"W | Present | Rivas et al. 2018; EBRG |
| 1993 | Venezuela | Uquire, Península de Paria | 10 | 10°42'34.0"N; 61°58'22.0"W | Present | EBRG 2585 |



Can artificial retreat sites help frogs recover after severe habitat devastation? Insights on the use of “coqui houses” after Hurricane Maria in Puerto Rico

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Abstract.—On September 2017, Hurricane Maria swept over Puerto Rico as a Category 4 storm. Severe canopy loss, augmentation of forest floor debris, and a significant increase in temperature and light reaching the understory were among the most evident changes at El Yunque National Forest, where a population of *Eleutherodactylus coqui* frogs has been monitored over the past 30 years. When sampling was re-established, the frogs could be heard calling, but it was very difficult to find them among the complexity of vegetation in the forest floor. We inferred that canopy disturbance had left frogs without optimal arboreal habitats for retreat, nocturnal perching, feeding, and reproductive activities, and wondered whether they would use artificial habitats placed in the forest understory. To test this, two types of artificial habitats (i.e., “coqui houses”) were introduced in the forest understory, consisting of either open PVC pipes or single-entrance natural bamboo shoots. Surveys were conducted twice a month for 15 months in an experimental transect with coqui houses, and a control transect without them. Data were collected on the occupancy rate of the artificial sites, type of usage, time of day occupied, and the number of *E. coqui* observed. The effects of time since the hurricane, microhabitat temperature, type of coqui house, and seasonality on the occupancy rate were also evaluated. Results showed that coquis used bamboo houses mostly during daytime as retreat and nesting sites, whereas the PVC houses were used mostly at night as calling sites. Daytime occupancy of coqui houses showed a significant bell-shaped pattern over time since the hurricane. This may be explained by a steady increase in usage after severe forest damage, a peak during the stressful cool-dry season, and a decline afterwards as the forest began to recover. No differences were found in frog counts between experimental and control transects, probably because the coquis could also hide among the fallen vegetation, but either disparities in forest conditions or inappropriateness of the methods for estimating population numbers may have overshadowed this effect. Coquis used artificial houses more often during the most stressful environmental conditions, suggesting that these shelters may serve to enhance habitat quality for amphibians after extreme weather events.

Keywords. Amphibians, conservation, *Eleutherodactylus*, extreme events, habitat augmentation, retreat sites

Citation: Burrowes PA, Hernández-Figueroa ÁD, Acevedo GD, Alemán-Ríos J, Longo AV. 2021. Can artificial retreat sites help frogs recover after severe habitat devastation? Insights on the use of “coqui houses” after Hurricane Maria in Puerto Rico. *Amphibian & Reptile Conservation* 15(1) [General Section]: 57–70 (e274).

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Accepted: 6 December 2020; **Published:** 14 June 2021

Introduction

Trends of recent climate change (1961–2010) in the Caribbean region show evidence of an increase in the frequencies of warm days, warm nights, and extreme high temperatures with a corresponding decrease of their cooler equivalents (Stephenson et al. 2014). An increase in minimum temperatures is significant at regional (Peterson et al. 2002; Stephenson et al. 2014) and local scales, such as the Puerto Rican eastern highland forests (Burrowes et al. 2004). While precipitation patterns for

the Caribbean are not as clear, some studies have shown a significant drying trend (Nurse and Sem 2001; Neelin et al. 2006). In addition, the frequency of extreme events, like hard rains and hurricanes, has increased significantly in the last decade, and the International Panel for Climate Change (IPCC) anticipates further increases in the future (Peterson et al. 2002; IPCC 2014, 2018; Oppenheimer et al. 2019). Due to factors intrinsic to the biology and physiology of amphibians, these patterns of climate change represent a threat to these animals. For example, many tropical ectotherms are thermoconformers, having

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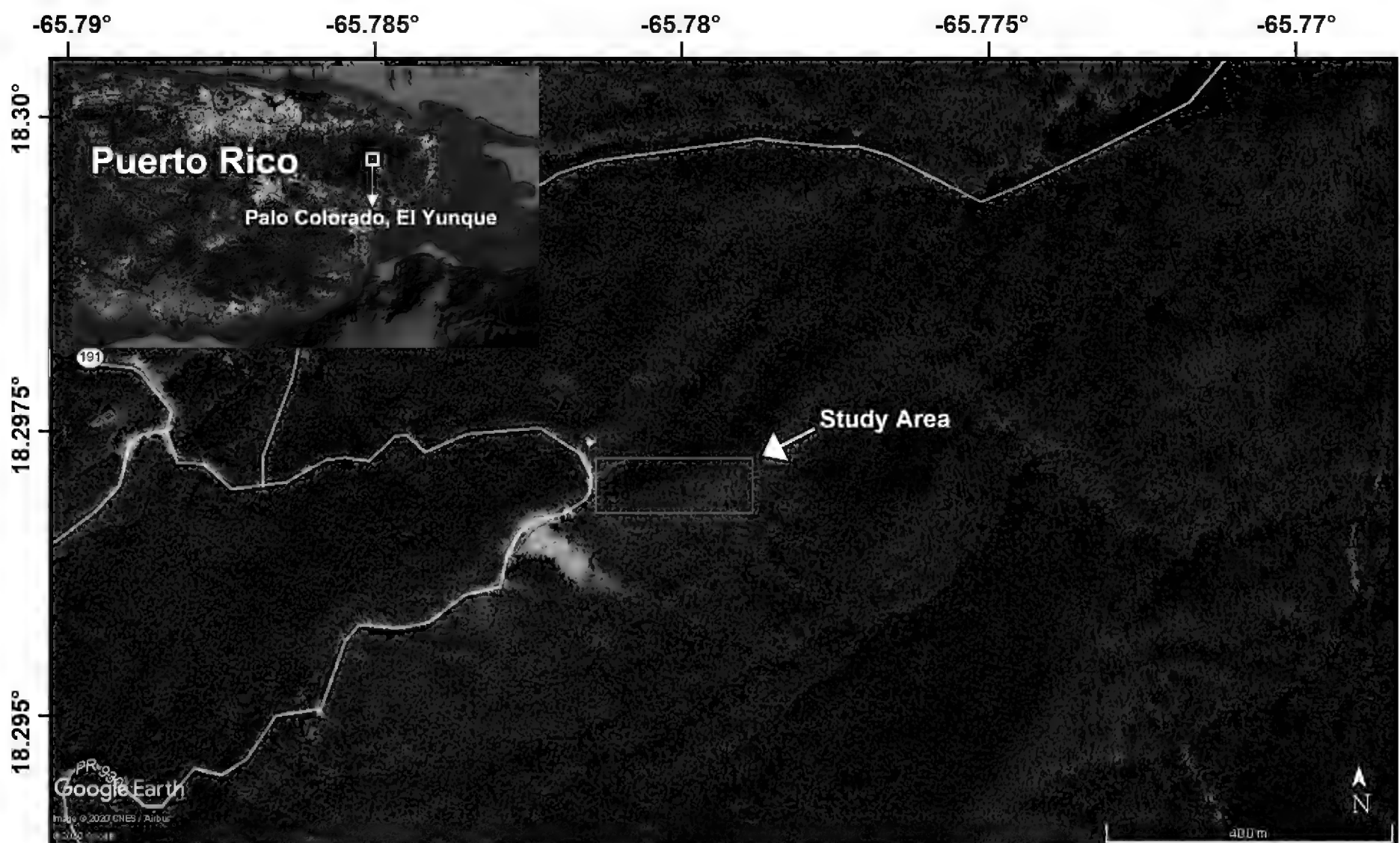


Fig. 1. Map showing the location of El Yunque National Forest in Puerto Rico, and the location of the study transects.

a reduced ability to thermoregulate compared to other vertebrates adapted to the climatic heterogeneity of higher latitudes (Navas 1996a,b; Huey et al. 2009). For the anurans in the genus *Eleutherodactylus*, which represent an important component of the endemic vertebrate fauna of the Caribbean (Hedges 1999; Duellman 1999; Joglar 2005), this may pose an additional challenge because amphibians lack epidermal protection that can reduce evapotranspiration rates during hot days. Thus, global climate change patterns for the Caribbean pose a risk for the *Eleutherodactylus* of Puerto Rico (locally known as “coquis”), which are already dealing with other threats such as the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis* Longcore, Pessier and Nichols, 1999) that causes chytridiomycosis (Burrowes et al. 2004, 2008a,b, 2017; Longo and Burrowes 2010; Longo et al. 2013).

Extreme atmospheric events, such as strong hurricanes, can affect coqui populations by changing local temperature regimes and habitat structure. A study on the effect of Hurricane Hugo (Category 3 in 1998) on a population of *Eleutherodactylus coqui* at the Luquillo Experimental Forest (LEF) of Puerto Rico, revealed an increase in adults, albeit at a smaller body size, and a decrease in juveniles (Woolbright 1991, 1996). The proliferation of adults was attributed to a greater availability of retreat sites among the fallen debris and a decrease in invertebrate predators, while the reduction of juveniles was explained by a decrease in reproductive activity due to changes in microclimate (Woolbright 1991). Another study experimentally evaluated the effect of two consequences of hurricanes, canopy disturbance and increased

deposition of debris in the forest floor, on a population of coquis in the LEF in Puerto Rico (Klawinski et al. 2014). In contrast to the results of Woolbright (1991), this study found that while canopy disturbances were detrimental to *E. coqui* abundance in experimental plots, an increase in forest debris had no effect (Klawinski et al. 2014).

In September 2017, Hurricane Maria hit Puerto Rico as a strong Category 4 storm with maximum sustained winds of 155 mph (~250 km/hr). High energy winds spread at 280 km/hr over the island along with heavy rainfall resulting in catastrophic flooding in many areas (NOAA 2017). As a consequence, critical damage to the island’s infrastructure occurred and Puerto Rico was declared a disaster area by the Federal Emergency Management Agency (FEMA). Natural ecosystems were also severely affected. At El Yunque National Forest in the eastern highlands of the island (Fig. 1), most large trees were defoliated and lost medium to large branches, while others were snapped or uprooted by Hurricane Maria’s strong winds. A large amount of vegetative debris accumulated on the forest floor causing an increase in structural complexity at that level. These changes and other complex consequences of hurricanes to ecosystems were discussed by Lugo (2008). Considering the negative effects of Hurricane Hugo on *E. coqui* populations (Woolbright 1991; Klawinsky et al. 2014), and with the knowledge that Hurricane Maria had been much stronger, we were concerned about the response of the population of coqui frogs that we have been monitoring for over 30 years at higher elevations in El Yunque National forest (Burrowes et al. 2004; Longo and Burrowes 2010).

We obtained permission from the U.S. Forest Service to evaluate our working area at El Yunque in December 2017, but due to security measures, we were not allowed to conduct nocturnal work in the forest until March 2018. At that time, finding our transects and clearing a path through forest debris to re-establish amphibian monitoring was arduous work. Initial surveys of the coqui population revealed that male frogs were still calling, but adults were difficult to observe because they were not active in their typical understory nocturnal sites, and juveniles, common in pre-hurricane surveys, were undetected. This was probably due to the absence of arboreal vegetation such as bromeliads and palm-frond axils which fell with the hurricane winds, as well as the loss of moss-covered tree trunks and branches that were concealed by leaves overhanging from the canopy before the hurricane, providing ideal hiding places for active frogs. Thus, the objective of this study was to provide artificial habitat in the form of “coqui houses” in the forest understory and quantify how much the frogs would use them for their regular activities, as well as the factors that may be associated with their usage. The data obtained could also serve to evaluate the potential of this strategy as a mitigation tool in the face of severe forest devastation.

The placement of artificial habitats has been used to increase reproductive activity and success of other vertebrate species of conservation concern. For example, Grubb and Bronson (1995) used artificial nesting sites made of PVC tubes to increase reproductive activity and success of Passeriformes birds (chickadees) in Ohio, USA. They found that when using artificial nesting sites, the survival of juveniles of one species of chickadees increased to 100%, and that birds used artificial nesting sites even in areas where natural nesting sites were abundant (Grubb and Bronson 1995). In Baja California, ospreys were observed using artificial nesting sites within a development area, resulting in an increase in reproductive activity and population size (Ortega-Rubio 1995). For the European Storm Petrels, for which the abundance of nesting sites is considered a limiting factor, the placement of artificial nesting sites proved to be effective at increasing population growth and density (De León and Mínguez 2003). Among amphibians, a study in Australia showed that water dams in farmlands supported a similar number of species as natural ponds, and highlighted the role of well-designed artificial habitats in frog conservation (Hazell et al. 2004). In Puerto Rico, Stewart and Pough (1983) placed artificial nest houses constructed from bamboo shoots in selected plots at “El Verde” in the LEF (350 m asl), and studied their effect on a population of *Eleutherodactylus coqui*. The authors found that the bamboo houses were often used as retreat and nesting sites, and resulted in significant increases in reproductive activity and population numbers. They concluded that retreat sites were a limiting factor for *E. coqui* population abundance (Stewart and Pough 1983).

Based on the positive results obtained by Stewart and

Pough (1983), we expected that coqui frogs confronting the habitat devastation caused by Hurricane Maria would use artificial habitats placed on trees in the forest understory as retreat, calling, perching, mating, and nesting sites. If so, we hypothesized a consequent increase in nocturnal frogs counts in experimental versus control transects because the coqui houses would encourage reproductive activity. The factors that influenced occupancy rate and the type of uses given to different types of artificial coqui houses were also investigated in an attempt to determine their potential effectiveness for mitigating the effects of habitat loss. Understanding the patterns of species responses to dramatic changes in habitat is important in order to develop effective conservation practices (Gascon 1993). The results of this work may guide future management strategies to help the recuperation of amphibians and/or other species after severe forest damage due to extreme climatic events.

Materials and Methods

Study Area

This work was conducted at El Yunque National Forest at 661 m asl in the Luquillo mountains of Puerto Rico. The study transects were located within the Palo Colorado Forest formation (18°18'5.8"N, 65°47'7.4"W; Fig. 1), characterized by the tree with the same name, *Cyrtilla racemiflora*, as well as the Sierra Palm, *Prestoea montana* (Ewel and Whitmore 1973; Harris et al. 2012). Other species, such as *Micropholis garcinifolia* (Caimitillo Verde), *Calycogonium squamulosum* (Jusillo), and *Croton poecilanthus* (Sabinón), are also common trees in the Palo Colorado Forest, and epiphytic bromeliads in the genus *Guzmania*, which are an important habitat for *Eleutherodactylus* frogs (Joglar 1998), are abundant (Stephenson et al. 1999; Harris et al. 2012). The average minimum temperature (nocturnal) and daily precipitation at the Palo Colorado Forest are 21.5 °C and 9.9 mm, respectively, but vary with the marked seasonality of Puerto Rico—being cooler and drier from January to April and warmer and wetter from May to December (Longo et al. 2010). Three species of *Eleutherodactylus*, *E. coqui*, *E. hedricki*, and *E. portoricensis*, can be found within the transect in the Palo Colorado forest. Following Hurricane Maria in 2017, the transect sites within this forest exhibited considerable canopy cover change. Table 1 shows an attempt to broadly categorize the stages of forest damage and chronological recuperation based on field notes and photographs (Fig. 2). The initial damage level was approximately 90–99% devastation, with a large proportion of that being vegetation accumulated in the forest floor, which then progressed to a considerable recuperation of up to 50% of the canopy cover by the end of 2019. The chronology presented in Table 1 may seem rather rapid, but research has shown that forest recovery after hurricane damage is faster in the tropics than in temper-

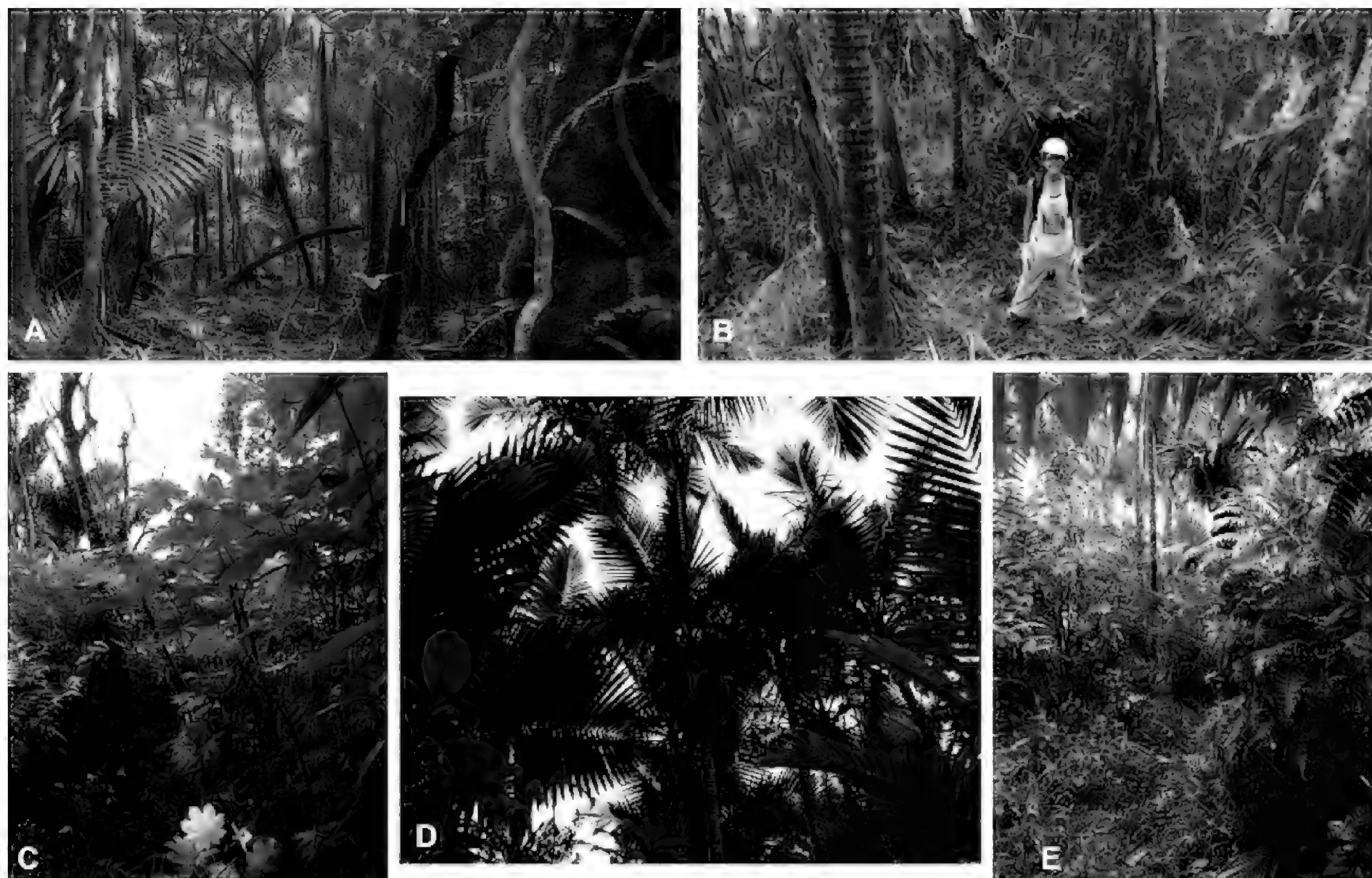


Fig. 2. Change in forest structure in the Palo Colorado forest transect (El Yunque) due to Hurricane Maria and corresponding damage/recovery stages according to Table 1. **(A)** Before the hurricane. **(B)** Same site after the hurricane, stage 1. **(C)** Moderate recuperation, stage 3. **(D–E)** Canopy dominated by Sierra Palm fronds showing signs of further recuperation of original understory vegetation, stage 4.

ate zones (Canham et al. 2010). In Puerto Rico, forests tend to recover basic structure within 10 to 20 years after hurricane blowdowns (Walker 1991; Lugo and Helmer 2004), and may achieve a tree size and density similar to those of primary forests after 40 years of recovery (Aide et al. 1996).

Study Species

The biology and ecology of *E. coqui* (Fig. 3) was extensively reviewed by Joglar (1998); thus, only some details that are pertinent to this study will be highlighted here. The species is native to Puerto Rico where it is widely

Table 1. Stages of forest changes describing the timeline of hurricane damage and gradual recovery. These stages are based on personal observations and field notes during daytime monitoring of coqui-houses at the Palo Colorado Forest (661 m) in El Yunque, Puerto Rico.

| Stages of hurricane damage (1 = greatest) | Forest description | Approximate time-frame |
|--|--|------------------------------------|
| 1 | 90–99% of the forest canopy gone; remaining standing trees 90–95% defoliated; vegetation fallen from the canopy accumulated in the floor | Hurricane Maria, Sep 2017–Sep 2018 |
| 2 | 85–90% of the forest canopy gone; palm trees grow back their fronds; canopy vegetation decomposing and understory vegetation growth dominated by herbaceous vegetation and opportunistic fast-growing plants that tolerate sunlight; recuperation of standing trees very limited | Oct 2018–Jan 2019 |
| 3 | 70–85% of forest canopy gone; standing trees growing leaves on branches, and native understory vegetation becomes apparent with new saplings restricting light and limiting the growth of herbs and opportunistic plants | Feb 2019–May 2019 |
| 4 | 50–70% of forest canopy gone; standing trees recuperating leaves to about 70%, and native understory vegetation growing with new saplings at about 5 m high; forest understory clear of herbs and other light-loving plants; canopy dominated by sierra palm fronds | Jun 2019–Dec 2019 |



Fig. 3. *Eleutherodactylus coqui* perching on natural habitat. (A) Female on branch. (B) Male on tree trunk.

distributed from urbanized to pristine areas, and from sea level to highland wet forests (0–1,189 m asl). It is an important nocturnal predator which consumes a variety of prey, predominantly arthropods (Woolbright 1991). The size of *E. coqui* varies considerably with the elevation, with individuals from higher elevations being the largest (Narins and Smith 1986). At the study site (661 m asl), the mean size of adult females measured as the snout-to-vent length (SVL) is 46.4 mm and that of adult males is 36.4 mm (Joglar 1998). Similar to other *Eleutherodactylus* species in Puerto Rico, *E. coqui* females are larger, presumably due to the cost of producing clutches of heavily-yolked, direct-developing eggs (Townsend and Stewart 1986; Woolbright and Stewart 1987). The common coqui uses various substrates as daytime retreats, including leaf litter, rock cavities, palm axils, and bromeliads. As nesting sites, they may use arboreal bromeliad axils, cracks within the bark of tree trunks, curled palms fronds, or large *Cecropia* leaves. It is common to observe males calling at night from vegetation 1–3 m above the ground. Reproductive activity is present all year around, but it is more frequent during the warm-wet season (Woolbright and Stewart 1987; Joglar 1998). During mating encounters, males call to attract females to a protected nesting site where amplexus takes place. Mating behavior usually lasts between 8.5–12 hours, and in contrast to most anurans, eggs are fertilized internally (Townsend et al. 1981). Males offer parental care to the clutch, which can last from 16 days in the higher temperatures typical of

lowlands, or up to 27 days in cooler, highland temperatures (Townsend and Stewart 1986).

Field Work

For this study, two 50 m x 3 m transects were sampled, an experimental transect where coqui houses were placed, and a control left unmanaged, approximately every two weeks for 15 months from August 2018 to October 2019. These transects are located only 100 m apart at the study site and have been monitored over many years to estimate population fluctuations and study the responses of coqui frogs to chytridiomycosis (Burrowes et al. 2004, 2017; Longo et al. 2010; Longo and Burrowes 2010). Visual encounter surveys were used to count the number of adult frogs active from the middle of the transects to a distance of 1.5 m at each side of the forest (Heyer et al. 2014) while also monitoring coqui houses for occupancy. Both transects were sampled simultaneously starting shortly after dusk (1830–1900 h) for approximately 2.5 hours by two or three trained people. This time range was chosen because it is the peak time of activity for *E. coqui* (Drewry 1970; Woolbright 1985). If a frog was found in one of the coqui houses, its behavior was recorded to infer the particular uses made of the artificial habitats, such as for retreat, calling, mating, or nesting and parental care. To determine potential differences in occupancy of coqui houses during daytime versus nighttime, coqui houses were checked twice, first at approxi-



Fig. 4. Artificial coqui houses built with (A) bamboo shoots and (B) PVC tubes.

mately 1600 h and then at night during the regular survey as described above. Juvenile frogs (SVL 5–18 mm) were not considered for this study because debris and invasive plant vegetation heavily covered the forest floor and the lower vegetation where young coquis are active at night (Burrowes et al. 2017). Thus, it was impossible to say with certainty whether juveniles truly decreased, or if their absence was an artifact of the difficulty in sampling.

Two different kinds of “coqui houses” (Fig. 4) were used: (A) bamboo houses made of natural bamboo cylinders cut at a node to provide a floor and a small opening carved into the lower part of the cylinder as a single entrance point (Stewart and Pough 1983); and (B) open-ended, hollow, white PVC pipes. The length of the cylinders for both kinds of houses was 6.4 cm, and the diameter did not exceed 4 cm. The top of the bamboo houses was closed with strong duct tape such that frogs could not get in or out, but they could be easily checked for occupancy by peeling the tape back (Fig. 4). In the experimental transect, a total of 22 bamboo houses and 22 PVC houses were deployed. One of each type was placed every 5 m in the understory, tied to trees or branches 1.5–2.0 m above ground in the forest understory (Fig. 4). Similar types of coqui houses are used to trap invasive *E. coqui* in Hawaii (Control of Coqui Frogs in Hawaii 2008; Pitt et al. 2012).

In order to document the changes in temperature associated with forest cover loss after Hurricane Maria and the structural damage caused to the forest canopy, HOBO® data-loggers were used to monitor ambient air temperature in the understory of the transects dur-

ing the 15 months of this study. Because microhabitat temperatures are routinely monitored with dataloggers for other studies in these transects, one datalogger was deployed during the hurricane that allowed us to track the temperature changes during the storm itself (Fig. 5A).

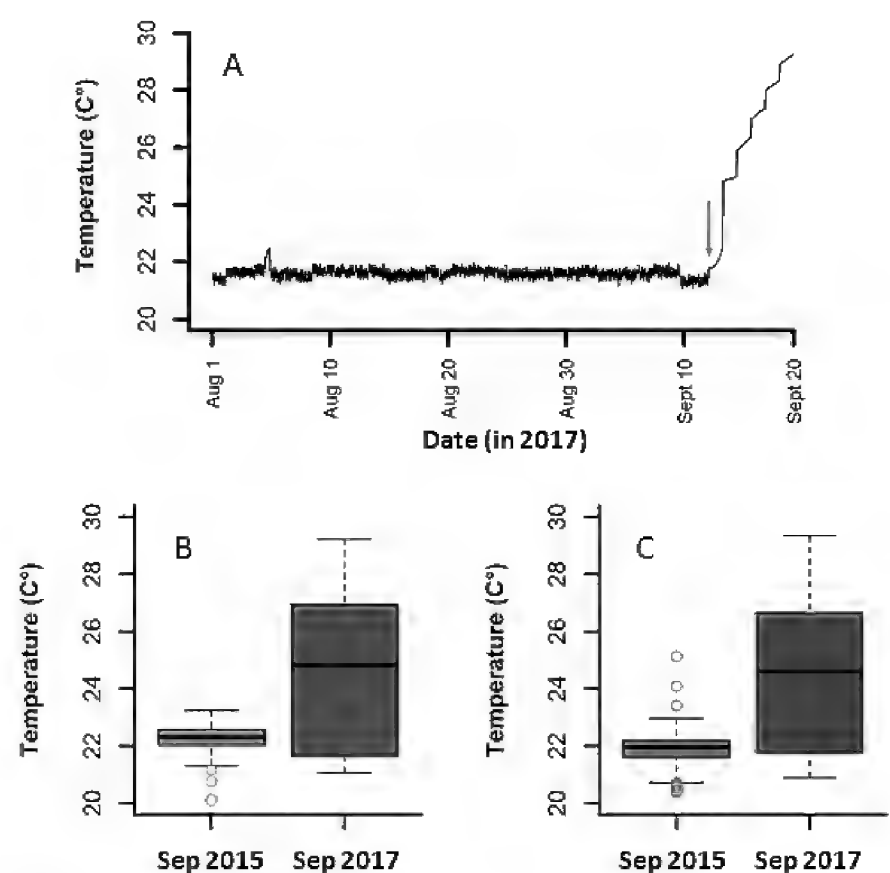


Fig. 5. Drastic changes in temperature at the transects in the Palo Colorado forest of El Yunque as a consequence of Hurricane Maria. (A) Ambient temperatures registered by HOBO data logger in the forest understory before, during, and shortly after Hurricane Maria. (B–C) Box plots showing variation in forest microhabitat temperature by day and at night during the month of September in 2015 (a non-hurricane year), and in 2017, the year that Hurricane Maria hit Puerto Rico.

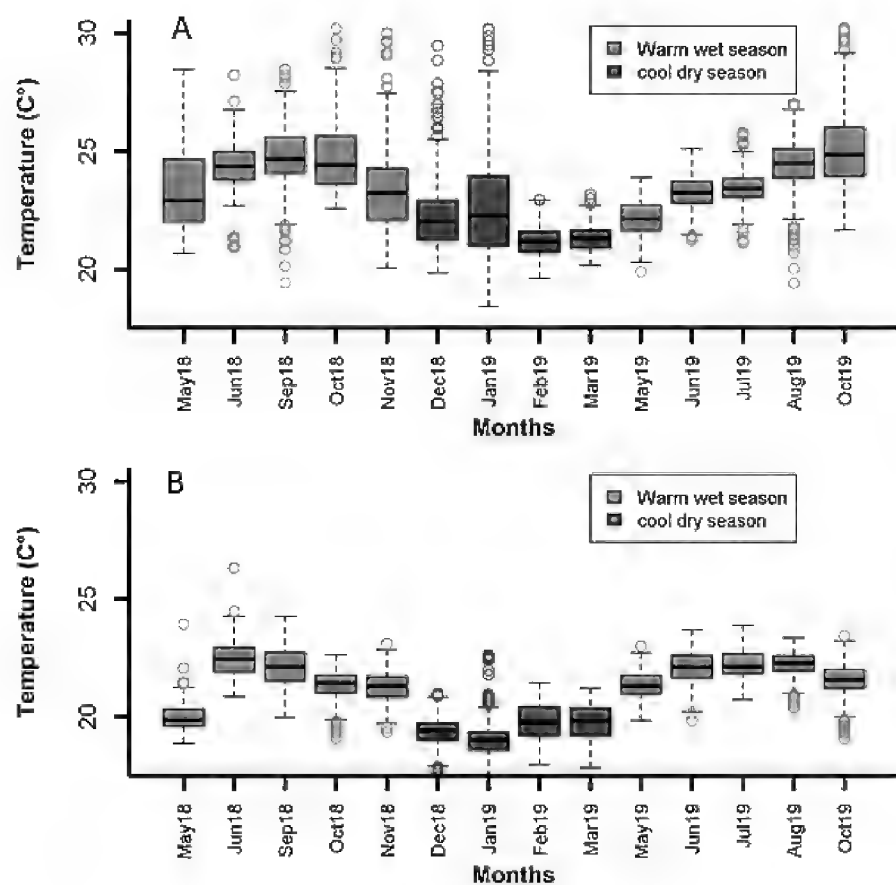


Fig. 6. Variation in operative temperatures measured by frog agar models in typical forest microhabitats after Hurricane Maria, showing a significant decrease during the cool-dry season (in blue) during midday (A), and nighttime (B).

The HOBO® data-loggers were also used in the bamboo coqui houses to record microhabitat temperature in the forest understory during the duration of this study. The thermal coupler was inserted into agar models designed to mimic coqui frogs (Rowley and Alford 2010; Burrowes et al. 2020) such that the microhabitat temperatures would reveal the operative temperatures that frogs would encounter at these sites (i.e., equilibrium body temperatures that the animal experiences in its habitat (Bakken and Gates 1975)). Temperature readings taken in the same manner in this transect during the year 2015 allowed the assessment of changes in the specific months before and after Hurricane Maria.

Analyses

Bar graphs are used to illustrate the frequency of usage of coqui houses by type and time of day through the sampling surveys or time since the hurricane, and boxplots are used to illustrate changes in temperature patterns. A Generalized Mixed Linear Model (GLM) was applied to evaluate factors that best predicted occupancy rates of the artificial habitats. In the model, date of sampling and coqui house number were considered random effects, and time (days) since Hurricane Maria, microhabitat temperature (mean of five days: four days immediately before and sampling day), and the type of coqui house (PVC versus bamboo) as fixed effects. Mann-Whiney or *t*-tests were conducted to test for differences in temperature in forest habitat that may be attributed to post hurricane damage, and ANOVA was used to determine whether mean frog counts were associated with transects where coqui houses were placed and whether differences in mean microhabitat temperatures were associated with seasons. Chi-square was used to test for independence

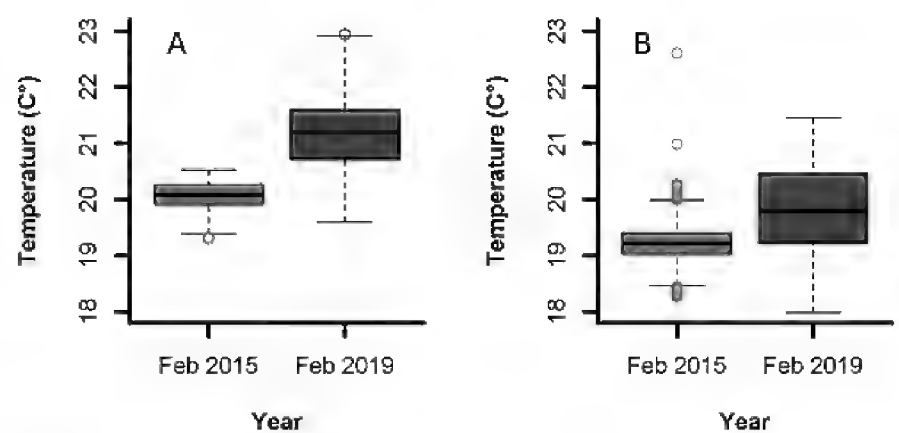


Fig. 7. Box plots showing variation in forest microhabitat temperature by day (A) and night (B) during the cool-dry season (February) of 2015 (a non-hurricane year), and in 2019, 17 months after Hurricane Maria hit Puerto Rico.

on the type of coqui house used by day versus night, as well as particular behaviors. Finally, a quadratic regression model was fitted to evaluate the predictive effect of time since the hurricane on the daytime usage of coqui houses. Statistical analyses were performed with Minitab Release 1.5.3 (<https://www.minitab.com/>) and R statistical package (<http://www.R-project.org/>).

Results

Temperature Changes in the Forest

As an immediate result of canopy cover loss due to Hurricane Maria, a drastic increase in the ambient temperature was registered by a data logger left in the forest until its battery was drained shortly after (Fig. 5A). In the microhabitats, a significant increase and high variability in temperature was found when comparing a non-hurricane year (September 2015) with that of September 2017, the year of Hurricane Maria (Fig. 5B–C). This pattern was evident both at mid-day when frogs are in retreat sites ($W = 46,697$, $P < 0.001$), and at night when they are active ($W = 310,949$, $P < 0.001$) (Fig. 5B–C). Temperature data taken during this study showed that after Hurricane Maria, frogs confronted operative temperatures spanning 22–28 °C during midday, and 18–24 °C at night in forest microhabitats (Fig. 6A–B). These temperatures are alarming because they were measured at retreat sites where frogs are protected from direct sunlight, and yet, are on average 2 °C higher than air temperatures registered in a previous study during 2005–2007 in the same forest transects (Longo et al. 2010). As expected, microhabitat temperatures post-Maria were significantly associated with seasonal changes, where higher temperatures corresponded to the warm-wet season and lower temperatures to the cool-dry season ($F = 79.47$, $df = 13$, $P < 0.001$; Fig. 6A–B). A comparison of the mean operative temperatures recorded in the same manner in February 2015 during the cool-dry season of a non-hurricane year, with those of February 2019 (17 months after Hurricane Maria), showed a significant increase in the microhabitat temperature during the day ($\bar{x} = 1.08$, $T = -5.34$, $df = 300$, $P < 0.0001$) and at night ($\bar{x} = 0.56$, $T = -11.09$, $df = 368$, $P < 0.0001$) (Fig. 7A–B).

Coqui frogs and Hurricane Maria

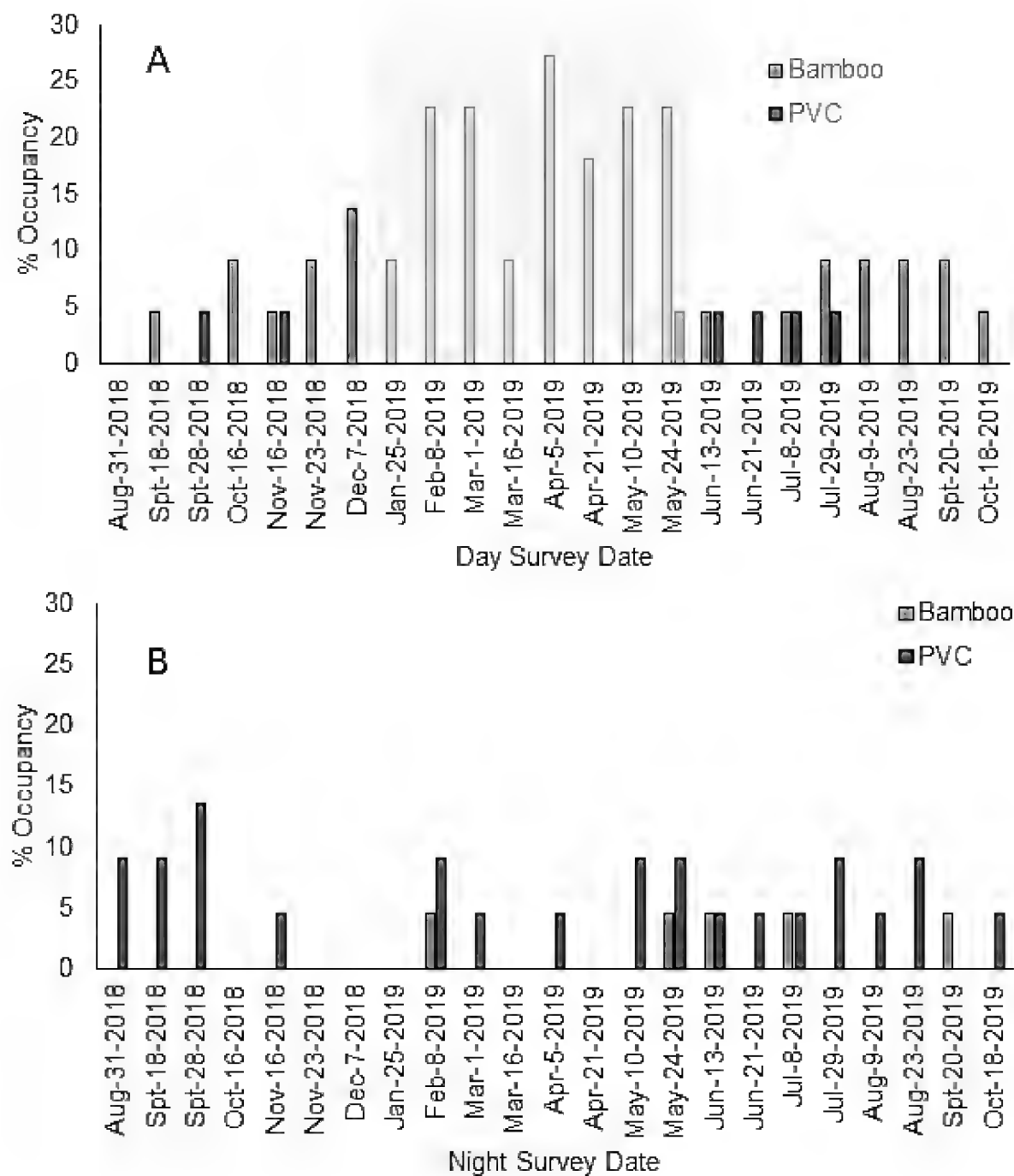


Fig. 8. Bar graphs showing coqui house occupancy rate by *Eleutherodactylus coqui* during the length of this study by daytime (A), and by nighttime (B) surveys. The shaded area in (A) denotes sampling in months during the cool-dry season.

Coqui House Occupancy Rates

The results of a general mixed model revealed that (1) time since the hurricane as a proxy of forest recovery, (2) microhabitat temperature, (3) house type, and (4) the interaction between time since the hurricane and microhabitat temperature were all significant predictors of occupancy rate of artificial coqui houses by *E. coqui* (Table 2).

Over the study period frogs that used these artificial habitats were found more often during the day with an occupancy rate up to 27.3% (mean 10.64, SD \pm 4.23), and somewhat less during the night with a maximum occupancy of 13.6% (mean 4.94, SD \pm 2.20) during any

sampling event (Fig. 8). The time at which frogs occupied one of these artificial habitats was not independent of the type of coqui house ($X^2 = 104.05$, df = 1, $P < 0.001$). Bamboo houses were used mostly during the day, as retreat and nesting sites, while PVC houses were used mostly at night for perching and/or calling ($X^2 = 115.94$, df = 1, $P < 0.001$, Fig. 9).

The number of frogs occupying coqui houses during the day was found to be inversely related to the mean midday (1200–1600 h) temperature at the microhabitats ($Y = -0.68x + 18.35$, $P = 0.0185$ and $R^2 = 37.13$). Accordingly, frogs occupied bamboo coqui houses significantly more often in the cooler dry season (shaded box) than in the warmer wet months ($F =$

Table 2. Results of Generalized Mixed Linear Model (GLM) to determine the effects of several factors on occupancy of the artificial coqui houses. The number of asterisks (*) indicates the level of statistical significance ($\alpha = 0.05$).

| Fixed effects | Estimate | Standard error | Z value | P (> z) | |
|-------------------------------|----------|----------------|---------|----------|-----|
| Intercept | -38.21 | 6.549 | -5.835 | 0.000 | *** |
| Time (days since hurricane) | 0.068 | 0.0097 | 6.937 | 0.000 | *** |
| Temperature | 1.525 | 0.277 | 5.496 | 0.000 | *** |
| House type PVC | -1.323 | 0.519 | -2.546 | 0.011 | * |
| Time: temperature interaction | -0.003 | 0.0004 | -7.221 | 0.000 | *** |

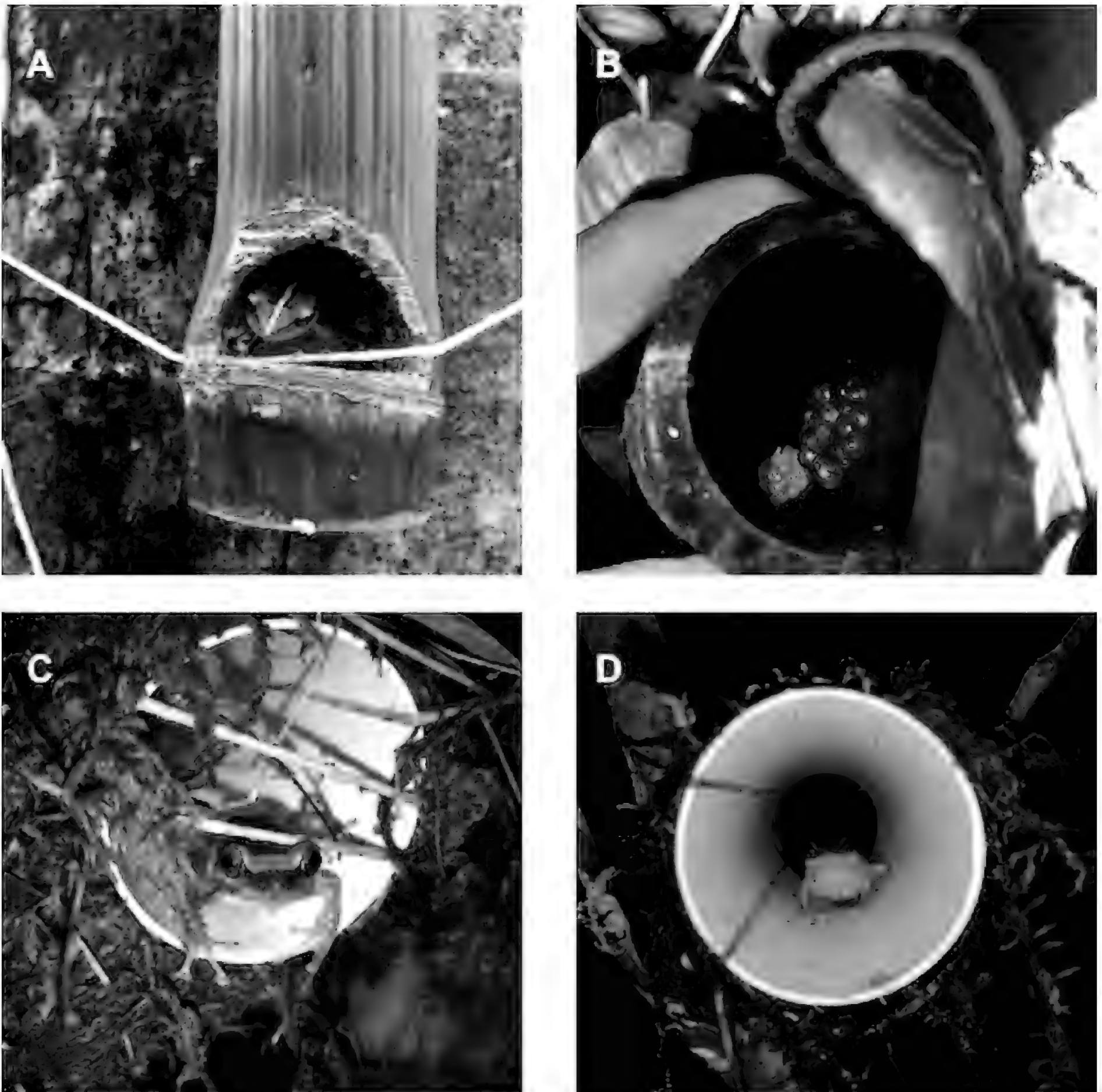


Fig. 9. Different uses ascribed to the two types of artificial habitats (=coqui houses) placed in the forest. **(A)** Coqui frog using bamboo house as retreat site during the day. **(B)** Bamboo house used as nesting site with a double clutch. Note that eggs are observed but the guarding male jumped away as the photo was taken. **(C)** PVC house used by a coqui as a nocturnal perching site. **(D)** PVC house used by a coqui as a calling site during the night.

5.90, $df = 13$, $P = 0.0258$, Fig. 8A). The frequency of daytime usage (i.e., occupancy rate) of coqui houses through time since the hurricane, which serves as a proxy of forest recovery (Table 1), fits a bell-shaped curve that was explained by a quadratic model ($y = -0.0004x^2 + 0.426x - 102.24$, $P = 0.0026$ and $R^2 = 0.40$, Fig. 8A). No pattern in the nocturnal usage could be associated with time after the hurricane; nonetheless, the coqui houses (especially PVC) were used consistently throughout the study (Fig. 8B). On four occasions, bamboo houses were used for nesting/parental care, and during this period the males stayed inside day-and-night for approximately 27 days until the eggs hatched and the juveniles dispersed (Fig. 9).

Contrary to what we expected, the mean number of adult frogs observed per survey night was slightly greater in the control transect (18.43 ± 5.98) than in the experimental transect (17.93 ± 5.54 ; Paired $T = -0.313$, $P = 0.7599$; Fig. 9). The higher variance associated with the abundance of frogs in the control transect may reflect greater habitat heterogeneity in this part of the forest (Fig. 10).

Discussion

Hurricanes have many effects on forest ecosystems, ranging from the physical damage to the forest and its functional consequences to biodiversity and ecosystem

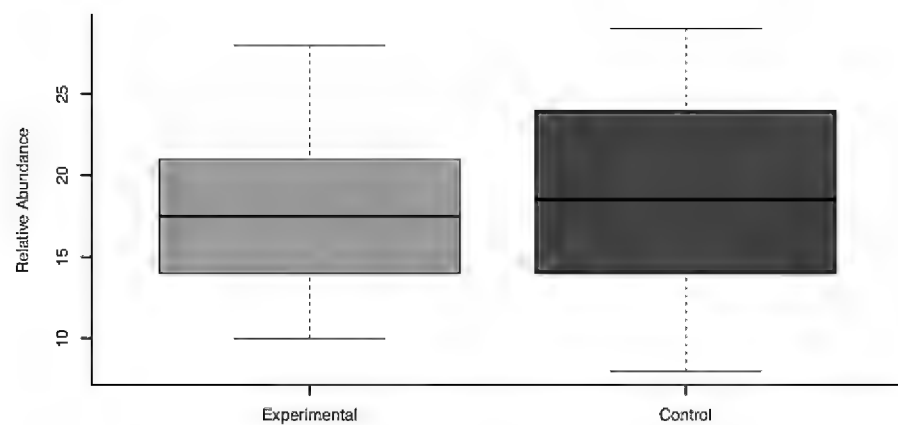


Fig. 10. Comparison of the relative abundance, measured as the number of adult *Eleutherodactylus coqui* observed per sampling night in the experimental transect where artificial coqui houses were made available, versus the control.

processes, to the opportunity for evolutionary change (Lugo 2008). Herein the thermal and structural changes that Hurricane Maria caused to a highland forest in Puerto Rico are documented, and results are presented on the responses of coqui frogs to the placement of artificial coqui houses on trees in the forest understory from which their traditional habitat had been displaced.

The drastic effect of Hurricane Maria's blowdown over the study site at El Yunque was evidenced by a 6 °C increase in ambient temperature in September 2017, right after it passed over Puerto Rico (Fig. 5A). A comparison of microhabitat temperatures in the months of September 2015, 17 years since the previous hurricane (Georges in 1998) and September 2017, show a significant increase in temperature attributable to the loss of forest canopy caused by Hurricane Maria (Fig. 5B–C). A similar comparison of microhabitat temperatures in the months of February in 2015 and 2019 (Fig. 7A–B), revealed that 17 months after the hurricane, when the forest is considered to be on recovery stage 3 (Table 1), frogs in the understory still confronted operational body temperatures approximately 1.0 °C higher than in non-hurricane years. The observed increase in temperatures by day and night associated with the loss of canopy are expected to bring about an increase in wind speed and a corresponding decrease in relative humidity within the forest (Tanner et al. 1991; Lugo 2008). These thermal changes may exacerbate the already stressful environmental conditions for coqui frogs as their operative body temperatures rise and the risk of dehydration from evaporative water loss increases. The fine interaction between local temperature and its impact on the frog's ability to maintain moisture is a key to amphibian homeostasis (Navas 1996a,b) and may result in unpredictable outcomes (Burrowes et al. 2020). In fact, temperature was a significant predictor of coqui house occupancy (Table 2), and the data revealed that frogs occupied artificial habitats significantly more often during the cool-dry season (Fig. 7A, shaded box). Low temperatures and drought are unfavorable conditions for tropical frogs, especially terrestrial direct-developers that depend on ambient moisture for rehydration (Duellman and Trueb 1994; Navas 1996b). Studies in Puerto Rico have shown that both nocturnal activity and

reproduction of *E. coqui* decrease during the dry season (reviewed by Joglar 1998) and that dry periods negatively affect their response to pathogens such as the chytrid fungus (Longo et al. 2010). Thus, we infer that the use of artificial retreats, such as the bamboo houses provided in this study, may have contributed to mitigating the effects of the hurricane.

Bamboo houses by day had a higher occupancy rate (Fig. 8), suggesting that the need for arboreal understory habitat that would serve as daytime retreat and nesting site was of higher demand than the nocturnal perching sites for which the PVC houses were used (Fig. 9). Thus, the results show that although coquis can survive hurricane devastation by hiding in the complexity of fallen vegetation (Woolbright 1991), they will use arboreal habitat if available. The preference for the more enclosed and protected bamboo houses during the daytime (when temperatures are higher, and the risk of dehydration is greater) is expected under the devastated canopy conditions caused by Hurricane Maria. Although PVC houses were used less often (Table 2), they were used at night throughout this study, often at an occupancy rate of 10% (Fig. 8B), suggesting that these open cylinders provided a sheltered perching site that may also benefit coqui males by, for example, amplifying calling sound at a time when other natural microhabitats were unavailable (Fig. 9).

Time since the hurricane, which is a proxy of forest recuperation, was also a predictor of the occupancy rate of coqui houses (Table 2), resulting in a significant bell-shaped response in daytime usage (see Fig. 8A). A rapid increase in usage at the beginning of the study, despite a potential learning curve to discover the “new habitats,” highlights the role of coqui houses in providing arboreal retreats and nesting sites soon after hurricane damage (recovery stages 1–2, Table 1). However, the peak in frequency of usage occurs later, in the midst of the cool-dry season when environmental conditions are most stressful to the frogs (Fig. 8A, shaded box). The gradual decrease in usage by the end of the study may be related to forest structure recovery since the hurricane. This pattern is confirmed by the significant interaction of temperature and time since the hurricane as predictors of the occupancy rate of artificial coqui houses (Table 2). With field notes and photographs, a chronological succession of the forest was documented, from over 90% canopy depletion to the recovery of foliage in standing trees to over 70%, and then to the replacement of invasive understory vegetation by native saplings that contribute more structure and shade by the end of 2019 (Table 1, Fig. 2). As the forest recuperates from the initial severe damage, restored natural habitat in standing trees is expected to serve as appropriate calling, perching, retreat, and nesting sites, and thus, the frogs would have a lesser need to occupy artificial habitats.

The rate of usage of bamboo houses by coqui frogs after Hurricane Maria (13–27%) was similar to that found in other studies that were successful in using artifi-

cial nesting sites as conservation methods. For example, Grubb and Bronson (1995) obtained 25% usage with the Carolina Chickadee birds in Ohio, USA; and in Benidorm, Spain, the European Storm Petrels used 29% of the artificial nesting sites (De León and Mínguez 2003). However, in Puerto Rico, a previous study showed that coqui frogs used up to 46% of the bamboo houses placed to enhance habitat in the lowland forests (Stewart and Pough 1983). With that amount of usage in undamaged forest (Stewart and Pough 1983), we expected to see a greater effect of artificial houses on the abundance of coquis in the experimental transect versus the control after Hurricane Maria. However, this was not the case (Fig. 10) probably because retreat sites are not a limiting factor for coquis after hurricane disturbances (Woolbright 1991). The increase of vegetative debris on the forest floor may have provided hiding places that were good alternatives to arboreal sites, allowing the frogs to cope with the other stressful conditions that the lack of canopy imposed. Other methodological caveats of this study may have contributed to the inability to show an effect of coqui houses on the number of frogs active at night. Since quantitative methods were not used to accurately compare the degree of canopy devastation between transects immediately after the hurricane, it is possible that the control transect had better conditions for the coquis in terms of perching, retreat, and reproduction sites than the experimental transect. It is also plausible that the number of coqui houses provided in this study was too few; while 44 coqui houses were set in 150 m², Stewart and Pough (1983) placed 100 of them in 100 m² plots. A greater number of artificial habitats may be needed, perhaps as a threshold, before a positive impact on population numbers can be observed. Finally, visual encounter surveys may not be the best way to count frogs after hurricane devastation of the habitat, particularly for a generalist species like *E. coqui*, because adults and especially juveniles can hide amongst the fallen debris where they would remain undetected.

Conclusions and Perspectives

This project aimed to determine whether a tropical forest frog population affected by an environmental catastrophe, such as a category 4–5 hurricane, would use artificial habitats set to augment arboreal forest structure. The findings reveal an increase in the forest temperature as a consequence of canopy blowdown, provide a description of the initial damage and early recovery stages of the forest (Table 1, Fig. 2), and highlight the importance of time since the hurricane, local climate, and the type of habitat on the frequency of usage of artificial habitats by coqui frogs. Although the data did not confirm that this kind of management intervention would result in an increase in the number of frogs, they did show that artificial habitats were used, and that occupancy rate increased significantly during the most stressful environmental conditions,

i.e., early after the hurricane and during the cool and dry season (Fig. 7A), which highlights their potential as a mitigation strategy after extreme events. Unfortunately, we missed the opportunity to study the immediate effects of Hurricane Maria on coqui frog populations because safety reasons prevented us from sampling in our transects for several months. Thus, whenever safe and feasible, we recommend beginning studies on the impact of environmental disasters as soon as possible in order to record the full range of their consequences and the responses of the organisms in question.

Acknowledgements.—Our work was conducted under permits from The Department of Natural and Environmental Resources of Puerto Rico-PR (DRNA: 2018-IC-067) and Institutional Animal Care and Use Committee (IACUC: 3012-05-23-2018). Alberto López kindly provided the photo of the male *E. coqui*. We acknowledge support from NSF grant (IOS-2011281) to P.A. Burrowes, and we are grateful to the many students from University of Puerto Rico who helped conduct field work, especially J. Peña, I. Ramírez, and P. Delgado.

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Amphibian diversity of a West African biodiversity hotspot: an assessment and commented checklist of the batrachofauna of the Ivorian part of the Nimba Mountains

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Abstract.—This article provides the first assessment and commented checklist of the anuran diversity of the Ivorian part of the Mount Nimba Integrated Nature Reserve (MNINR), West Africa. During a period of 81 days from 18 June 2018 to 17 May 2019, covering both the rainy and dry seasons, 53 amphibian species were recorded. Among these species, 30.2% were endemic to either the Upper Guinea forest zone or smaller areas within that biodiversity hotspot. The amphibian fauna of the Ivorian slope of the MNINR is very similar to those of the Guinean side of Mounts Nimba and the Guinean Simandou Range. Based on the current IUCN Red List data, several recorded species are of high conservation concern: the Critically Endangered *Nimbaphrynoides occidentalis*; the Endangered *Hyperolius nimbae*; and the Near Threatened *Leptopelis macrotis*, *Leptopelis occidentalis*, and *Odontobatrachus arndti*. Of particular interest among the survey records were the poorly known *Ptychadena arnei*, *P. pujoli*, and *P. submascareniensis*. The records of *Ptychadena retropunctata* and *Arthroleptis cruscum* represent first country records for Ivory Coast, while the records of *Odontobatrachus arndti* and *Phrynobatrachus fraterculus* are the second records for the country. In contrast to the Guinean and Liberian parts of Mounts Nimba, the Ivorian part had never been mined or explored for mining, nor do such plans currently exist. As a result, the study area still holds intact mountain forests that include rare and unique habitats with exceptional biodiversity, which need to be preserved for future generations. Consequently, conservation strategies should minimize bush-fires in mountain grasslands, e.g., to protect the viviparous toad *N. occidentalis*. At lower elevations, it is important to encourage local activities concerning reforestation of the previously forested areas and the conservation of the (sacred) village forests.

Keywords. Anura, conservation, endemics, first record, Ivory Coast, UNESCO World Heritage Site, taxonomy, Upper Guinea forest

Citation: Kanga KP, Kouamé NG, Zogbassé P, Gongomin BAI, Agoh KL, Kouamé AM, Konan JCBYN, Adepo-Gourène AB, Gourène G, Rödel MO. 2021. Amphibian diversity of a West African biodiversity hotspot: an assessment and commented checklist of the batrachofauna of the Ivorian part of the Nimba Mountains. *Amphibian & Reptile Conservation* 15(1) [General Section]: 71–107 (e275).

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Accepted: 28 April 2021; **Published:** 27 June 2021

Introduction

Worldwide habitat loss and the consequent decline of terrestrial vertebrates have particularly severe impacts on amphibians (e.g., Lips 1999; Raxworthy and Nussbaum 2000; Hero and Morrison 2004; Stuart et al. 2004; Crawford et al. 2010). Mountainous regions are particularly important areas for the conservation of amphibians since they provide a large number of different habitat types with high species richness. In particular, the species inhabiting the higher elevations are often range restricted or endemic (Herrmann et al.

2005; Kozak and Wiens 2010; Blackburn 2008; Juárez-Ramírez et al. 2016; Portik et al. 2016; Doherty-Bone and Gvoždík 2017; Khatiwada et al. 2019; van der Hoek et al. 2019; Bittencourt-Silva et al. 2020). This pattern also applies to the West African highlands, which host unique and remarkable amphibian species (Kouamé et al. 2007; Hillers et al. 2008a; Ofori-Boateng et al. 2018). The Upper Guinean forest zone of West Africa is among the most important global biodiversity hotspots (Myers et al. 2000). Within that ecoregion, the Mounts Nimba is situated on the borders between Liberia, Guinea, and Ivory Coast, and harbors a particularly large number of

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endemic species (Schnell 1952; Angel et al. 1954a,b; Lamotte and Sanchez-Lamotte 1999; Énard and Brosset 2003; Girard 2003; Ineich 2003; Roy 2003; Monadjem et al. 2013; Decher et al. 2016; Simmons et al. 2021). Thus, this mountain range, which abruptly rises from the surrounding plains up to an elevation of 1,752 m asl, is considered of ‘Exceptionally High Priority’ for the conservation of biodiversity in the Upper Guinea forest zone (Bakarr et al. 2001).

While the amphibian fauna of Mounts Nimba ranks among the most species rich and most intensively studied of the amphibian faunas in West Africa (Rödel et al. 2004), almost all research has been done on the Guinean and Liberian parts of the mountain range (e.g., Guibé and Lamotte 1958a,b, 1963; Xavier 1978; Rödel et al. 2010; Sandberger et al. 2010; Sandberger-Loua et al. 2018a; Schäfer et al. 2019), and none has ever focused exclusively on the Ivorian part of the mountains. One particular research focus was on the viviparous toad *Nimbaphrynoides occidentalis* (Angel, 1943), which is a flagship species for the conservation of the area (e.g., Lamotte 1959; Lamotte and Sanchez-Lamotte 1999; Hillers et al. 2008a; Xavier 2009; Sandberger et al. 2010; Sandberger-Loua et al. 2016, 2017, 2018b). However, although much research effort has been directed to the amphibian fauna of the Nimba Mountains, as indicated by the accumulation of tens of thousands of amphibian vouchers at the Muséum National d’Histoire Naturelle in Paris, new records and new species descriptions continue to be published from the Guinean and Liberian parts of Mounts Nimba (Rödel et al. 2009, 2010; Barej et al. 2015; Sandberger-Loua et al. 2018a). Thus, there is a pressing need to investigate the Ivorian part of the Nimba Mountains as well, and such research seems particularly urgent as the steadily increasing human population in the area is demanding access to land. As a result of armed conflicts in Ivory Coast and neighboring countries, a massive influx of refugees into the forested areas of western Ivory Coast is increasingly limiting the few remaining areas of primary rainforests (Woods 2003). The northern part of Mounts Nimba, shared between Guinea and Ivory Coast, received strict protection in 1944. The Ivorian part was gazetted as an UNESCO World Heritage Site in 1982, and declared the Mount Nimba Integrated Nature Reserve (MNINR) by the national law 2002-102 of February 2002, and the property was integrated into the public domain of Ivory Coast (Lauginie 2007). This paper presents the results of recent field surveys with the aim of providing a better understanding of the batrachofauna of the Ivorian sector of the Nimba Mountains, and this information will contribute to the long-term protection of this unique and biodiverse area.

Materials and Methods

Study area. Amphibian surveys were carried out in the Mount Nimba Integrated Nature Reserve (MNINR),

situated at the westernmost extension of the mountains in Ivory Coast (07°25’–07°45’N, 008°20’–008°35’W; Fig. 1). Covering 5,000 ha, the MNINR makes up only a small portion of the Nimba Mountains, while the largest part (12,540 ha) is located in Guinea. The highest peak of the Nimba Mountains is the Richard-Molard with an altitude of 1,752 m asl (Lamotte et al. 2003a,b; Lauginie 2007).

The varied geomorphology and the sub-equatorial climate, with strong seasonal and altitudinal differences, result in a variety of different microclimates. Fluctuations of mean annual temperatures range between 22–27 °C on the mountain bases to 16–21 °C on the peaks. Daily temperature fluctuations may span more than 20 °C during the dry season. Temperatures are lowest during the core rainy season from August to September, and reach highest values in March and April. The rainy season extends over eight to nine months, and is only interrupted by a short dry season from November/December to February/March. Annual precipitation varies considerably between the low and high elevations and is highest in the montane grasslands, where it may reach up to 3,500 mm. In the dry season a warm, dry and dusty wind, known as Harmattan, prevails (Lauginie 2007). Humidity in the rainy season usually exceeds 80%, but drops below 30% during Harmattan periods. The Nimba range is a water reservoir, and the source of more than 50 streams and rivers, among which the rivers Cavally, Gouè, and Nuon are of regional importance. During the rainy season, the montane parts of the mountains are mostly enveloped in clouds. The slopes are predominantly covered with dense evergreen forests at lower to mid-elevations, giving way to patches of moist savannah. Higher elevations (those above ~1,200 m asl) are dominated by montane grasslands on iron-ore ground (Lamotte 1998; Lamotte et al. 2003a,b; Lauginie 2007).

Survey sites. Four distinct habitat types are distinguished with different amphibian assemblages. Their definitions have been based on elevation and vegetation. Habitat A (Fig. 2) comprises montane grasslands present at the highest elevations. Habitat B (Fig. 3) is a mid-elevation savannah/grassland. An important species in the montane grasslands and mid-elevation savannah is *Loudetia kagerensis* (Poaceae), which grows on iron-oxide quartzite ground. These open habitats are frequently affected by fires during the dry season. Habitat C (Fig. 4) is dense, broadleaf and evergreen forests stretching from lower to mid-elevations (422 to 847 m asl). Torrent streams cross these mountain forests in ravines, and the water level of mountain streams decreases considerably during the dry season. Habitat D (Fig. 5) comprises altered, former forest habitat that is now inhabited predominantly by non-forest species. This area is close to Yéalé village, situated at 377 m asl, about 2 km from the periphery of the MNINR. The village area is bordered by islands of bamboo forests, partly intact forests, degraded forests with large clearings, and thick grassy

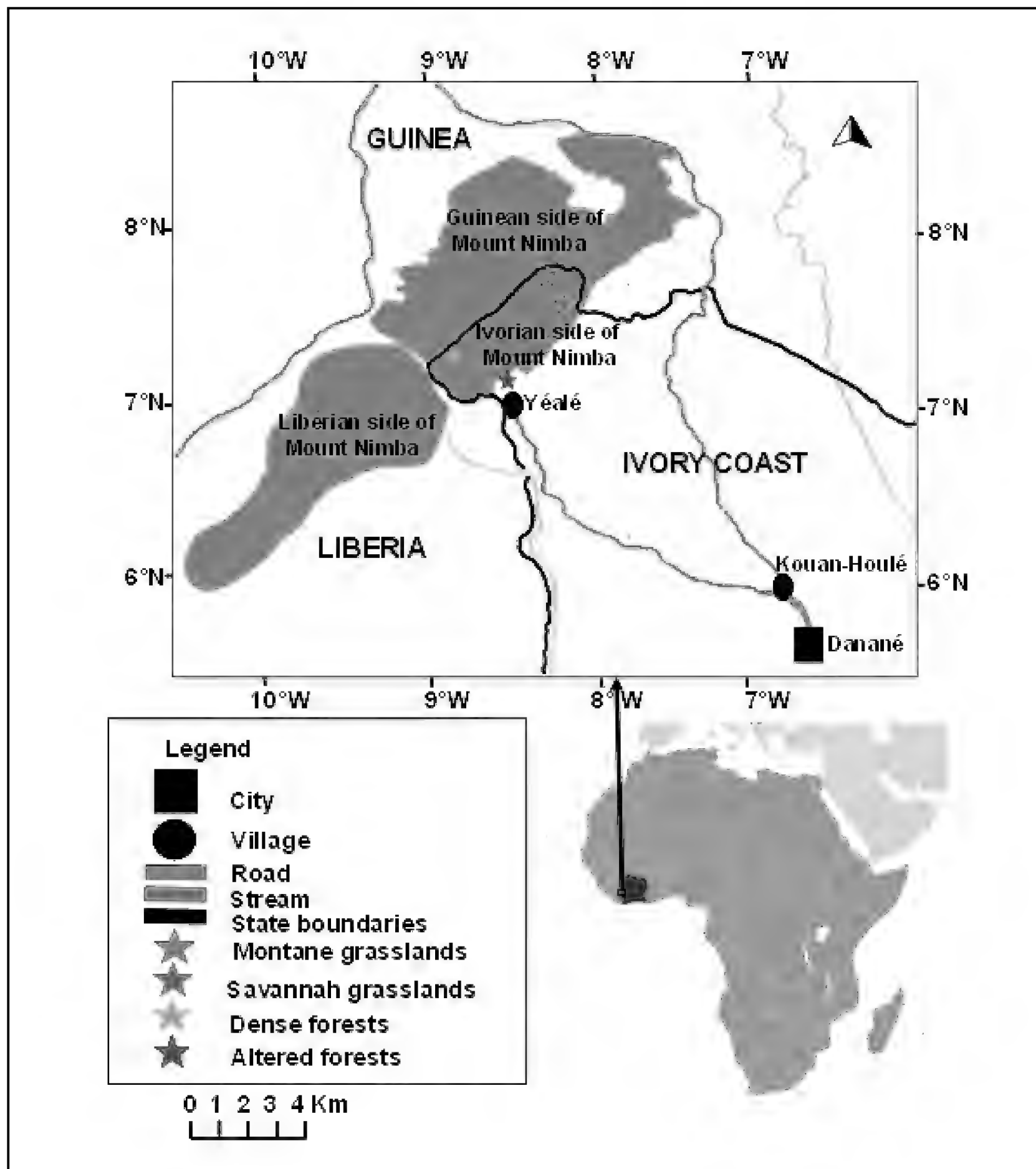


Fig. 1. Geographical location of the Mount Nimba Integrated Nature Reserve, within the westernmost extension of Ivory Coast at the border crossing point with Guinea and Liberia. Four distinct habitats with different amphibian assemblages based on altitudinal and vegetation types are indicated: Montane grasslands at the highest elevations (A: red star; Fig. 2); Mid-elevation savannah grasslands (B: purple star; Fig. 3); Dense, broadleaf and evergreen forests from lower to mid-elevations (C: orange star; Fig. 4); and Altered forests (D: green star; Fig. 5). The inset figure indicates the location of Ivory Coast (green patch) on the African continent.

and shrubby vegetation around houses. Cocoa and coffee plantations, small-scale subsistence farming, cultivating plantains, cassava, and corn, as well as swamps used for rice cultivation, dominate large parts of the village's surroundings.

Field work, sampling effort, and vouchers. Despite the absence of the panzootic chytrid fungus *Batrachochytrium dendrobatidis* (Bd) from West Africa west of the Dahomey Gap (Penner et al. 2013; Zimkus et al. 2020), as a precaution new or disinfected equipment

was always used on each survey. Animals were mainly found opportunistically through visual encounter surveys (Heyer et al. 1994; Rödel and Ernst 2004), supplemented by acoustic surveying, lifting logs and rocks, peeling away bark, scraping through leaf litter, tufts, grasses, and broad-leaved trees, and searching around or within water-filled tree holes. Furthermore, potential breeding sites were checked for tadpoles by dip-netting. Because amphibians were not marked, repeated observations of a given individual in multiple visits cannot be excluded. Surveys of all accessible habitats were conducted by

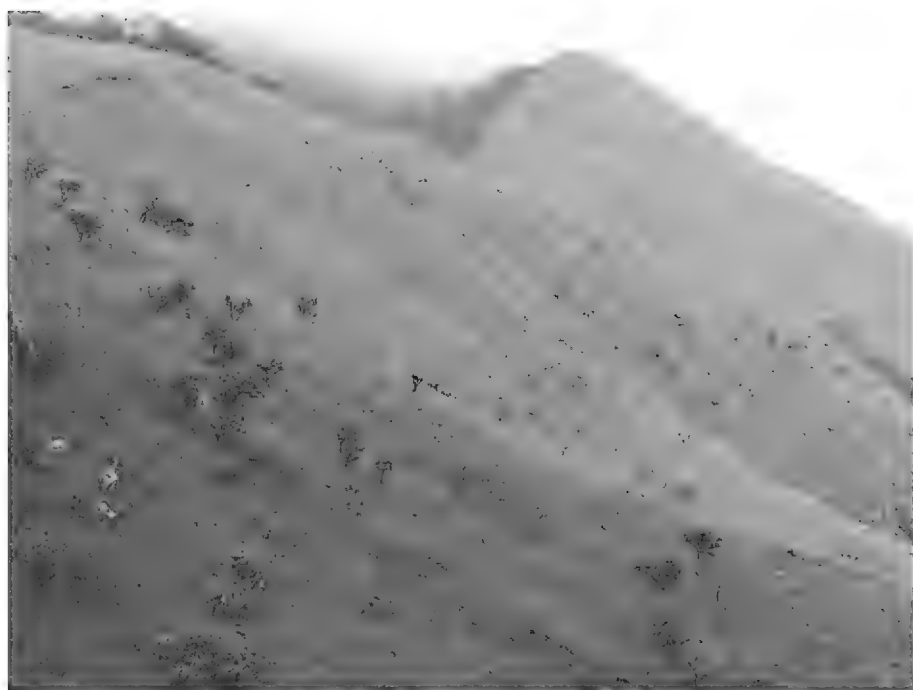


Fig. 2. Montane grasslands (habitat A) at 1,241 m asl.

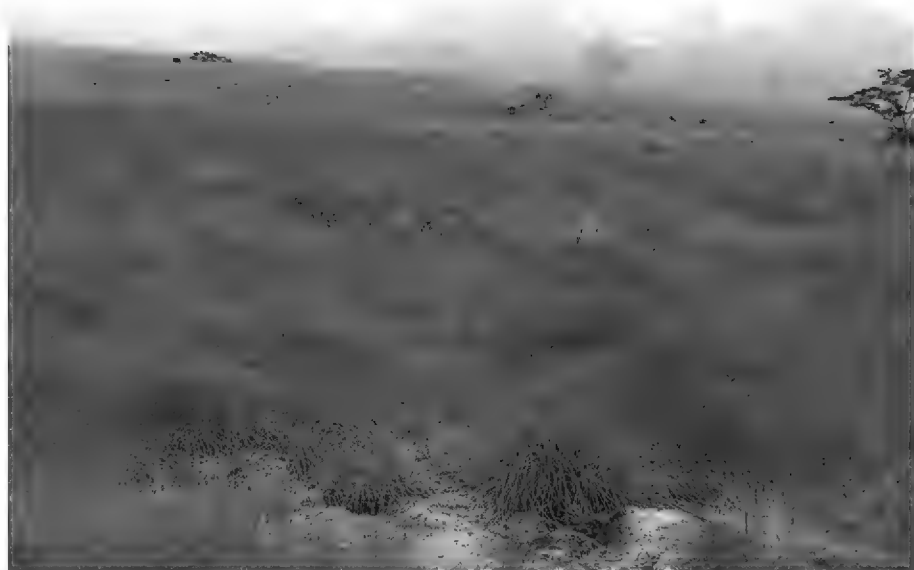


Fig. 3. Mid-elevation savannah (habitat B).

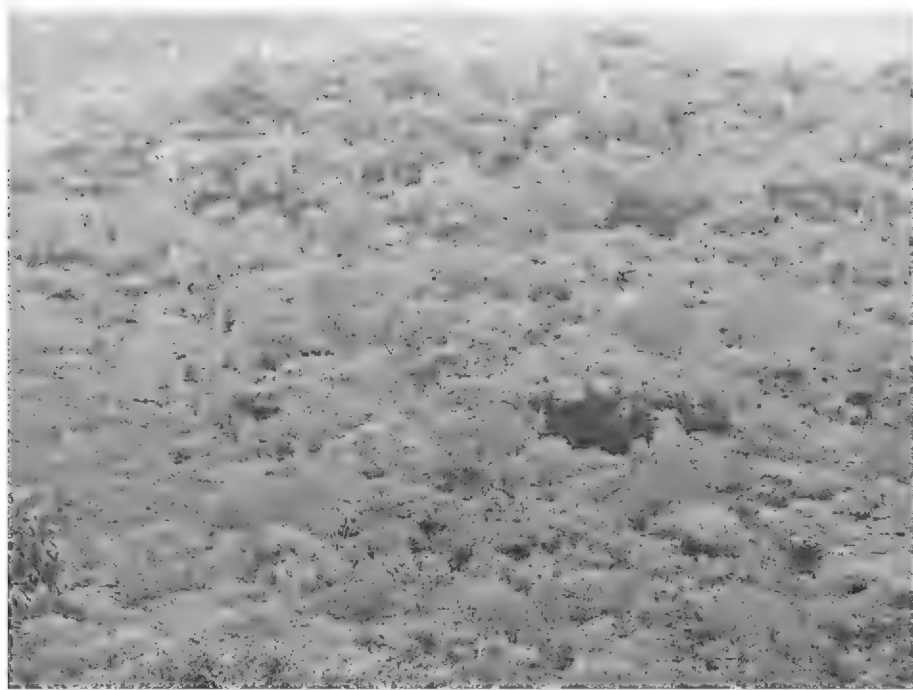


Fig. 4. Lower to mid-elevation dense, evergreen forest (habitat C) at 847 m asl.



Fig. 5. The Yéalé village at the foothills of Mounts Nimba showing altered former forest habitat (habitat D). The mountains are visible in the background.

five people during both day (0830–1230 h GMT) and night (1800–2200 h GMT). Field work was conducted in the rainy and dry seasons, and included a total of 81 days from 18 June 2018 to 17 May 2019. Habitats B, C, and D were each investigated 56 times (day and night) during the rainy season, and 25 times (day and night) in the dry season. The montane grasslands (A) were investigated 12 times in the rainy season and seven times in the dry season, both during daytime only (Table 1). Night searches could not be conducted in this habitat, as overnight stays were not possible, and descending the mountain at night was too dangerous.

The overall sampling effort involved 3,240 person-hours. The geographical coordinates using the WGS84 datum for each site were recorded with a hand-held GPS

device (Garmin 20 etrex). The observations for each species are summarized below, and the nomenclature used herein follows Channing and Rödel (2019). Amphibians were captured by hand and identified to species level. All individuals were photographed, measured, sexed, and if not retained as vouchers, released in their respective habitats. The symbols in “*” refer to records that probably comprises several species in the Tables and Appendix. Snout-urostyle-lengths (SUL) were taken with dial calipers (accuracy ± 0.5 mm). Voucher specimens were euthanized in a 1,1,1-trichloro-2-methyl-2-propanol hemihydrate (MS222) solution, preserved in 80% ethanol, and deposited at the Jean Lorougnon Guédé University, Daloa, Ivory Coast. The numbers of retained vouchers (NGK) are listed with the species accounts.

Table 1. Number of daily searches, during the 81 day period from 18 June 2018 to 17 May 2019, in each of the four habitat types (A, B, C, and D) in Mount Nimba Integrated Nature Reserve. The habitat types are described in the “Survey Sites” section in **Materials and Methods**.

| Habitat A | | | | Habitat B | | | | Habitat C | | | | Habitat D | | | |
|------------|-------|--------------|-------|------------|-------|--------------|-------|------------|-------|--------------|-------|------------|-------|--------------|-------|
| Dry season | | Rainy season | | Dry season | | Rainy season | | Dry season | | Rainy season | | Dry season | | Rainy season | |
| Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night | Day | Night |
| 5 | 0 | 12 | 0 | 25 | 25 | 56 | 56 | 25 | 25 | 56 | 56 | 25 | 25 | 56 | 56 |

Statistics. As most data were collected opportunistically (and are thus not strictly quantitative), only the Chao2 and Jackknife1 estimators, both based on presence/absence data and for all habitats, were used to calculate expected species richness and thus sampling efficiency, using the software EstimateS (Colwell 2006). Calculations were based on the daily species lists (81 days of survey work) for all 53 amphibian taxa recorded in MNINR. To avoid order effects, calculations were based on 500 randomized runs of the daily species lists. The Sørensen's similarity index (Π), which varies from 0 to 1 (Sørensen 1948; Wolda 1981), was used to determine species similarity between the four habitat types (A, B, C, and D). Likewise, Π was used for pairwise comparisons between species overlap with the MNINR (this study) and eight nearby and surrounding sites in the western part of the Upper Guinean hotspot that were previously surveyed (Chabanaud 1920, 1921; Parker 1936; Guibé and Lamotte 1958a, 1963; Laurent 1958; Schiøtz 1967; Taylor 1968; Böhme 1994a,b; Lamotte and Ohler 1997, 2000; Rödel 2003; Rödel and Ernst 2003; Rödel and Bangoura 2004; Rödel et al. 2004; Ernst et al. 2006; Hillers et al. 2008a; Barej et al. 2015; Sandberger-Loua et al. 2018; Schäfer et al. 2019). The *Hyperolius* sp. by Hillers et al. (2008a) from Fouta Djallon was *H. occidentalis* (N.G. Kouamé, pers. obs.). Because the intraspecific morphological variation of frogs from the West African *Arthroleptis poecilonotus*-complex (< 30 mm snout-urostyle length) overlaps with interspecific variation, it is currently not possible to distinguish these frogs at the species level based on morphological characteristics alone (Rödel and Bangoura 2004). Advertisement calls of our records hint that these squeaker frogs may actually represent several taxa, but are treated herein as one taxon, termed *Arthroleptis poecilonotus*-complex. Apart from *Hyperolius* sp., the records of frogs not identified to the species level were excluded from the calculations of the Sørensen index.

Results

Species Richness and Faunal Similarities

A total of 53 anuran species were recorded in MNINR. A list of all taxa with site records, known general habitat preferences, distribution range, and the current IUCN Red List category is provided in Table 2. Concerning range, our definition of West Africa follows Penner et al. (2011), i.e., a region extending from Senegal in the west to the Nigerian Cross River in the east. Using the estimators, we calculated 53 (sd: ± 0.62 ; Chao 2) and 54 (sd: ± 1.39 ; Jack-knife 1) anuran species to occur in the study area. Thus, we found almost the entirety of the species richness (100% and 96.29%, respectively) for the Ivorian sector of Mounts Nimba.

Approximately one-third (16 spp., 30.2%) of the recorded species are restricted to the Upper Guinean

forest zone, while another one-third (16 spp., 30.2%) are even further limited to the western part of this biodiversity hotspot. Two species (3.8%), *Hyperolius nimbae* and *Nimbaphrynoides occidentalis*, are endemic to the Nimba area; while eight species (15.1%) have a larger West African range. Eleven species (20.75%) are known to occur beyond West Africa (Table 2).

Over one-quarter of the species encountered (14 sp., 26.4%) require forest habitats. Among them, eight species (15.1%) are typical savannah specialists; five (9.4%) occur in farmbush (degraded forest) habitats, while 11 (20.8%) are known to inhabit savannah and farmbush habitats; nine (17%) are known from forest and savannah habitats; and two species (3.8%), *Phrynobatrachus gutturosus* and *Ptychadena arnei*, have been recorded across the entire broad habitat range from savannah and farmbush to forest (Table 2).

Concerning the habitat specific species richness in MNINR, the following species numbers were recorded in each of the four distinct habitats: four species in A, eight in B, 21 in C, and 32 in D. Two species (*Phrynobatrachus tokba* and *Ptychadena submascareniensis*) were common to habitats A and B, while three (*Astylosternus occidentalis*, *Sclerophrys maculata*, and *Phrynobatrachus tokba*) were common to B and C. Three species (*Leptopelis viridis*, *Sclerophrys maculata*, and *Hoplobatrachus occipitalis*) occurred in B and D, and five (*Arthroleptis poecilonotus*-complex, *Leptopelis macrotis*, *Sclerophrys maculata*, *Hyperolius chlorosteus*, and *Kassina cochranæ*) were found in C and D (Table 2). Habitat A showed the highest species overlap/similarity (Π -value: 0.33) with habitat B; habitat B shared a mean species overlap/similarity (Π -value: 0.21) with habitat C, and the lowest species overlap/similarity (Π -value: 0.21) with habitat D (Π -value: 0.15); while habitat C shared a low species overlap/similarity (Π -value: 0.19) with habitat D.

One species, *Phrynobatrachus tokba*, occurs in forest, farmbush habitats, and montane grasslands; another species (*Ptychadena submascareniensis*) inhabits savannah and montane grasslands; while two species (3.8%), *Arthroleptis cruscolum* and *Nimbaphrynoides occidentalis*, are confined to montane grasslands only (Table 2).

With respect to the IUCN status of threatened species, one species (*Nimbaphrynoides occidentalis*) is ranked as Critically Endangered; one species, *Hyperolius nimbae*, is listed as Endangered; four (*Arthroleptis cruscolum*, *Leptopelis macrotis*, *L. occidentalis*, and *Odontobatrachus arndti*) are Near Threatened; and four (*Hyperolius soror*, *Ptychadena arnei*, *P. pujoli*, and *P. submascareniensis*) are Data Deficient.

The results of the Sørensen's similarity index for pairwise comparisons between the MNINR (this study) and eight nearby and surrounding sites from the western part of the Upper Guinean hotspot are presented in

Amphibians of the Nimba Mountains (Ivorian part)

Table 2. Amphibian species recorded in the Mount Nimba Integrated Reserve with respective habitat records, known habitat preferences, distribution range, and IUCN Red List category. Habitats A, B, C, and D are described in the “Survey Sites” section in Materials and Methods. AF = Africa (any range beyond West Africa), WA = West Africa (defined as the area west of the Cross River in Nigeria), UG = Upper Guinea (defined as forest zone west of the Dahomey Gap), wUG = western Upper Guinea (defined as any range from western Ivory Coast or beyond the western part of this country), E = endemic to Mounts Nimba; S = savannah, MG = montane grasslands, FB = farmbush (degraded and secondary forest), F = forest; IUCN categories: LC = Least Concern, NT = Near Threatened, EN = Endangered, CR = Critically Endangered, NE = Not Evaluated by IUCN.

| Families and species | Habitats | | | | Distribution range | | | | | Habitat preferences | | | | IUCN Red List |
|---|----------|---|---|---|--------------------|----|----|-----|---|---------------------|----|----|---|---------------|
| | A | B | C | D | AF | WA | UG | wUG | E | S | MG | FB | F | |
| Arthroleptidae | | | | | | | | | | | | | | |
| <i>Arthroleptis cruscum</i> | X | | | | | | | X | | | X | | | NT |
| <i>Arthroleptis poecilonotus</i> -complex* | | | X | X | | | X | | | | | X | X | NE |
| <i>Astylosternus occidentalis</i> | | X | X | | | | | X | | | | | X | LC |
| <i>Cardioglossa occidentalis</i> | | | X | | | | X | | | | | | X | NE |
| <i>Leptopelis macrotis</i> | | | X | X | | | X | | | | | | X | NT |
| <i>Leptopelis occidentalis</i> | | | X | | | | X | | | | | | X | NT |
| <i>Leptopelis spiritusnoctis</i> | | | X | | | | X | | | | | X | X | LC |
| <i>Leptopelis viridis</i> | | X | | X | X | | | | | X | | X | | LC |
| Bufonidae | | | | | | | | | | | | | | |
| <i>Nimbaphrynoides occidentalis</i> | X | | | | | | | | X | | X | | | CR |
| <i>Sclerophrys maculata</i> | | X | X | X | X | | | | | X | | X | | LC |
| <i>Sclerophrys regularis</i> | | | | X | X | | | | | X | | X | | LC |
| <i>Sclerophrys togoensis</i> | | | X | | | | X | | | | | | X | LC |
| Conrauidae | | | | | | | | | | | | | | |
| <i>Conraua alleni</i> | | | X | | | | | X | | | | | X | LC |
| Dicroglossidae | | | | | | | | | | | | | | |
| <i>Hoplobatrachus occipitalis</i> | | X | | X | X | | | | | X | | X | | LC |
| Hemisotidae | | | | | | | | | | | | | | |
| <i>Hemius marmoratus</i> | | | | X | X | | | | | X | | | | LC |
| Hyperoliidae | | | | | | | | | | | | | | |
| <i>Afrixalus dorsalis</i> | | | | X | | X | | | | X | | X | | LC |
| <i>Afrixalus fulvovittatus</i> | | | | X | | | X | | | | | X | | LC |
| <i>Hyperolius chlorosteus</i> | | | X | X | | | | X | | | | | X | LC |
| <i>Hyperolius concolor</i> | | | | X | | | X | | | X | | X | | LC |
| <i>Hyperolius fusciventris fusciventris</i> | | | | X | | | | X | | | | X | | LC |
| <i>Hyperolius guttulatus</i> | | | | X | | X | | | | | | X | X | LC |
| <i>Hyperolius lamottei</i> | | X | | | | | | X | | X | | | | LC |
| <i>Hyperolius nimbae</i> | | | | X | | | | | X | | | X | | EN |
| <i>Hyperolius picturatus</i> * | | | | X | | | X | | | | | X | X | LC |
| <i>Hyperolius soror</i> | | | X | | | | | X | | | | X | | DD |
| <i>Hyperolius cf. sylvaticus</i> | | | | X | | | X | | | | | X | X | LC |
| <i>Hyperolius sp.</i> | | | | X | | | | X | | | | X | | NE |
| <i>Kassina cochranae</i> | | | X | X | | | | X | | X | | X | | LC |
| Odontobatrachidae | | | | | | | | | | | | | | |
| <i>Odontobatrachus arndti</i> | | | X | | | | | X | | | | | X | NT |
| Phrynobatrachidae | | | | | | | | | | | | | | |

Table 2 (continued). Amphibian species recorded in the Mount Nimba Integrated Reserve with respective habitat records, known habitat preferences, distribution range, and IUCN Red List category. Habitats A, B, C, and D are described in the “Survey Sites” section in Materials and Methods. AF = Africa (any range beyond West Africa), WA = West Africa (defined as the area west of the Cross River in Nigeria), UG = Upper Guinea (defined as forest zone west of the Dahomey Gap), wUG = western Upper Guinea (defined as any range from western Ivory Coast or beyond the western part of this country), E = endemic to Mounts Nimba; S = savannah, MG = montane grasslands, FB = farmbush (degraded and secondary forest), F = forest; IUCN categories: LC = Least Concern, NT = Near Threatened, EN = Endangered, CR = Critically Endangered, NE = Not Evaluated by IUCN.

| Families and species | Habitats | | | | Distribution range | | | | | Habitat preferences | | | | IUCN Red List |
|---------------------------------------|----------|---|---|---|--------------------|----|----|-----|---|---------------------|----|----|---|---------------|
| | A | B | C | D | AF | WA | UG | wUG | E | S | MG | FB | F | |
| <i>Phrynobatrachus alleni</i> | | | X | | | | X | | | | | | X | LC |
| <i>Phrynobatrachus annulatus</i> | | | X | | | | X | | | | | | X | LC |
| <i>Phrynobatrachus francisci</i> | | | | X | | X | | | | X | | | | LC |
| <i>Phrynobatrachus fraterculus</i> | | | X | | | | | X | | | | X | X | LC |
| <i>Phrynobatrachus guineensis</i> | | | X | | | | | X | | | | | X | LC |
| <i>Phrynobatrachus gutturosus*</i> | | | | X | | X | | | | X | | X | X | LC |
| <i>Phrynobatrachus latifrons</i> | | | | X | | X | | | | X | | X | | LC |
| <i>Phrynobatrachus liberiensis</i> | | | X | | | | X | | | | | | X | LC |
| <i>Phrynobatrachus natalensis</i> | | | | X | X | | | | | X | | | | LC |
| <i>Phrynobatrachus phyllophilus</i> | | | X | | | | X | | | | | | X | LC |
| <i>Phrynobatrachus tokba</i> | X | X | X | | | | X | | | | X | X | X | LC |
| Pipidae | | | | | | | | | | | | | | |
| <i>Xenopus tropicalis</i> | | | | X | | X | | | | | | X | X | LC |
| Ptychadenidae | | | | | | | | | | | | | | |
| <i>Ptychadena arnei</i> | | | | X | | | | X | | X | | X | X | DD |
| <i>Ptychadena bibroni</i> | | | | X | X | | | | | X | | X | | LC |
| <i>Ptychadena longirostris</i> | | | X | | | X | | | | | | X | X | LC |
| <i>Ptychadena oxyrhynchus</i> | | | | X | X | | | | | X | | X | | LC |
| <i>Ptychadena pujoli</i> | | | | X | | | | X | | X | | | | DD |
| <i>Ptychadena pumilio</i> | | | | X | X | | | | | X | | X | | LC |
| <i>Ptychadena retropunctata</i> | | X | | | | | | X | | X | | | | LC |
| <i>Ptychadena stenocephala</i> | | | | X | X | | | | | X | | | | LC |
| <i>Ptychadena submascareniensis</i> | X | X | | | | | | X | | X | X | | | DD |
| <i>Ptychadena tournieri</i> | | | | X | | X | | | | X | | | | LC |
| Ranidae | | | | | | | | | | | | | | |
| <i>Amnirana</i> sp. ‘albolabris west’ | | | | X | | | X | | | | | X | X | NE |
| Rhacophoridae | | | | | | | | | | | | | | |
| <i>Chiromantis rufescens</i> | | | | X | X | | | | | | | | X | LC |

Table 3. Among the Ivorian sites, the Taï National Park had the highest similarity (Π -value: 0.62) with MNINR concerning amphibian assemblage composition. More than half of the anuran fauna of MNINR was also shared with the Mount Sangbé National Park (Π -value: 0.58) and the Mount Péko National Park (Π -value: 0.54), two mountainous areas in western Ivory Coast. Naturally,

our survey area was most similar to the amphibian fauna of the Guinean part of Mounts Nimba (79% similarity). With 72% and 67% similarity, the Guinean Simandou range and Diécké Classified Forest likewise had faunas that were very similar to the MNINR. In contrast the Fouta Djallon, the westernmost part of the Upper Guinea highlands, comprising savannah, limited forest, and

Table 3. Sørensen’s Similarity Value (η) between the anuran fauna of the Mount Nimba Integrated Reserve and nearby and surrounding sites from the western part of the Upper Guinean hotspot of West Africa, including respective species richness. Area abbreviations: DCF = Diécké Classified Forest; FD = Fouta Djallon Highlands; MB = Mount Béro; MN = Mount Nimba; MP = Mount Péko National Park; MS = Mount Sangbé National Park; SR = Simandou range; ZCF = Ziamia Classified Forest. Literature records were adjusted to reflect recent taxonomic changes.

| Area | Species richness | Number of species common with this study | η -value (Sørensen) | Source |
|-------------------|------------------|--|--------------------------|---|
| MP (Ivory Coast) | 29 | 22 | 0.54 | Rödel and Ernst (2003) |
| MS (Ivory Coast) | 44 | 28 | 0.58 | Rödel (2003); Barej et al. (2015) |
| TNP (Ivory Coast) | 53 | 33 | 0.62 | Rödel and Ernst (2003); Ernst et al. (2006) |
| DCF (Guinea) | 39 | 31 | 0.67 | Rödel et al. (2004) |
| FD (Guinea) | 26 | 15 | 0.38 | Hillers et al. (2008a); Barej et al. (2015) |
| MB (Guinea) | 28 | 22 | 0.54 | Rödel et al. (2004) |
| MN (Guinea) | 56 | 43 | 0.79 | Guibé and Lamotte (1958a, 1963); Laurent (1958); Schiøtz (1967); Lamotte and Ohler (1997, 2000); Rödel et al. (2004); Barej et al. (2015); Sandberger-Loua et al. (2018); Schäfer et al. (2019) |
| SR (Guinea) | 52 | 38 | 0.72 | Parker (1936); Taylor (1968); Rödel and Bangoura (2004) |
| ZCF (Guinea) | 31 | 20 | 0.48 | Chabanaud (1920, 1921); Böhme (1994a,b) |

rivers with waterfalls, only shares 38% of the species with MNINR (Table 3).

Species Accounts

After each species name the numbers of retained vouchers (NGK-Nimba) are listed.

Arthroleptidae

Arthroleptis cruscum Angel, 1950

Evening Squeaker

Material: Two males, NGK-Nimba 0019, NGK-Nimba 0130 (Fig. 6A). **Comments:** On a rainy day they were found together with a juvenile Nimba Toad (*N. occidentalis*) below a stone in montane grassland (07°35.555’N, 008°25.788’W; 1,235 m asl). These males had an oval to slender elongated body and measured 15.5 and 21.0 mm SUL, respectively. *Arthroleptis cruscum* always possesses a granular to warty dorsal skin. Its habitat differs from other species of the genus which are present on Mounts Nimba. *Arthroleptis nimbaensis*, *A. langeri*, and *A. krokosua*, and occur in rainforest and/or farm bush (Guibé and Lamotte 1958b; Rödel et al. 2009; Adum et al. 2011; Nopper et al. 2012; Sandberger-Loua et al. 2018a). *Arthroleptis cruscum* occurs in high elevation grasslands up to 1,750 m asl during the rainy season and seems to survive the dry season in gallery forests and at the edges of marshes (Guibé and Lamotte 1958b).

Arthroleptis poecilonotus-complex

Mottled Squeaker

Material: Two males, NGK-Nimba 0021 (Fig. 6B),

NGK-Nimba 0022. **Comments:** These squeaker frogs were widespread in the forest area as well as in farmlands within the vegetation, where several concealed males emitted their insect-like chirping calls which cannot be assigned to any morphotaxa. They occurred from 425 to 847 m asl. A male of 23.0 mm in SUL was captured in a patch of forest and retained as voucher (07°35.233’N, 008°25.190’W; 847 m asl). Another male voucher (SUL 24.0 mm) was recorded in an agricultural area (07°31.928’N, 008°25.401’W; 425 m asl). *Arthroleptis poecilonotus*-complex are larger than *A. langeri* but smaller than *A. krokosua*. The two vouchers may comprise different species, of which one could be conspecific with *A. nimbaensis*. However, currently that cannot be clarified (see Rödel and Bangoura 2004; Channing and Rödel 2019). All of these *Arthroleptis* species, apart from *A. cruscum*, may have similar habitat requirements (Rödel et al. 2009; Adum et al. 2011; Nopper et al. 2012; Sandberger-Loua et al. 2018a).

Astylosternus occidentalis Parker, 1931

Western Night Frog

Material: Two males, NGK-Nimba 0014, NGK-Nimba 0023, and one female, NGK-Nimba 0024 (Fig. 6C). **Comments:** While *A. occidentalis* was previously mostly recorded in patches of lowland forests (Rödel and Branch 2002; Rödel and Bangoura 2002; Ernst and Rödel 2006; Hillers and Rödel 2007; Hillers et al. 2008b; Rödel and Glos 2019), on Mounts Nimba the species occurs in altitudinal forest habitats as well (Guibé and Lamotte 1958a). During the night several active individuals were detected among leaf litter in a patch of forest (07°35.233’N, 008°25.190’W; 847 m asl), close to

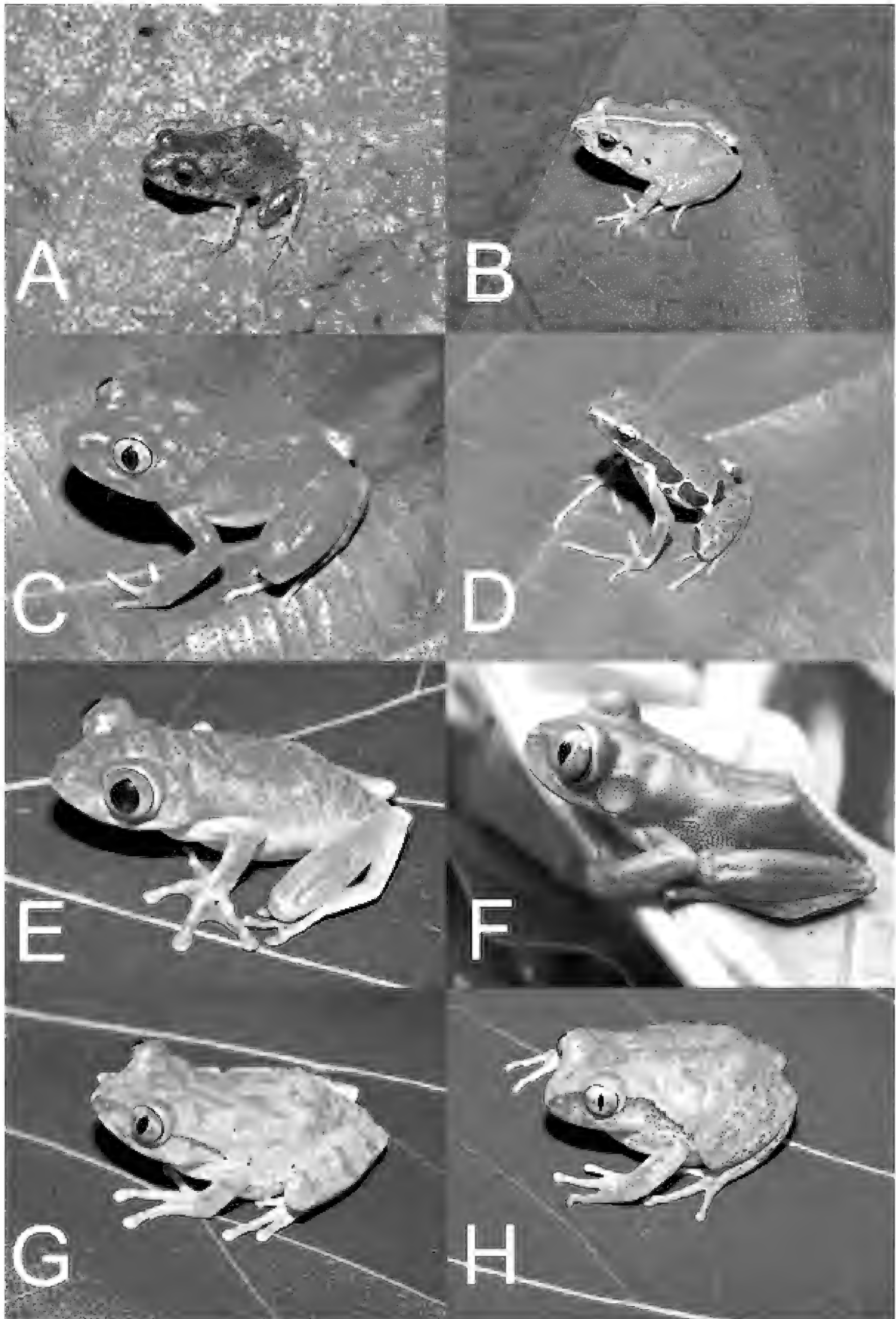


Fig. 6. Arthroleptid frogs from Mount Nimba Integrated Nature Reserve: *Arthroleptis crusculum* male (A); *Arthroleptis poecilonotus*-complex female (B); *Astylosternus occidentalis* female (C); *Cardioglossa occidentalis* male (D); *Leptopelis macrotis* male (E); *Leptopelis occidentalis* male (F); *Leptopelis spiritusnoctis* female (G); *Leptopelis viridis* female (H).

fast-flowing streams. Male SULs ranged from 45.0–50.2 mm (N = 3), while females measured from 46.0–61.0 mm (N = 9). The majority of specimens had a dark brown dorsum, although one female exhibited an orange color. In contrast to the general forest habitat requirements of this species we found some, presumably migrating, frogs at night, in the core rainy season near a crystal-clear stream in predominantly grassy savannah (07°35.453'N, 008°24.957'W; 843 m asl). During the day, they were hidden underneath stones.

***Cardioglossa occidentalis* Blackburn, Kosuch, Schmitz, Burger, Wagner, Gonwouo, Hillers, and Rödel, 2008**

Western Long-fingered Frog

Material: Three males, NGK-Nimba 0025, NGK-Nimba 0026 (Fig. 6D), NGK-Nimba 0027. **Comments:** *Cardioglossa occidentalis* is a nocturnal leaf litter frog, distributed along forest streams from Sierra Leone to Ghana (Rödel et al. 2001; Rödel and Branch 2002; Ernst and Rödel 2006; Blackburn et al. 2008; Hillers et al. 2008c). During the night, males frequently emitted insect-like calls (see Rödel et al. 2001), and were well concealed below leaf litter along forest streams. Three males were collected near a small stream running through a slightly degraded forest patch that was dominated by bamboo (07°32.993'N, 008°24.753'W; 425 m asl). Their SULs ranged from 27.0–29.0 mm.

***Leptopelis macrotis* Schiøtz, 1967**

Large-eared Tree Frog

Material: Three males, NGK-Nimba 0017, NGK-Nimba 0018, NGK-Nimba 0131 (Fig. 6E). **Comments:** *Leptopelis macrotis* is one of the largest species in the genus. It occurs in primary forests, preferentially at the edges of streams, from eastern Sierra Leone to Ghana (Schiøtz 1967; Rödel et al. 2014; Channing and Rödel 2019). In Ivory Coast, as in its entire range, the species is threatened due to forest degradation and conversion, e.g., two of its Ivorian sites (see Rödel and Branch 2002) have been recently converted into rubber plantations (P.J. Adeba, pers. comm.). During this survey, only three males of *L. macrotis* were recorded, two of which were found during the dry season. Both frogs (45.5 and 48.5 mm SUL) were perched on a branch of a broad leaf, at ~2.5 m height, close to a large stream (07°33.121'N, 008°25.036'W; 422 m asl). The third male (42.5 mm SUL), in contrast, was found in a degraded forest during the rainy season. This male was perched on a branch, at 75 cm above the ground, close to a large stream (07°31.932'N, 008°25.508'W; 387 m asl).

***Leptopelis occidentalis* Schiøtz, 1967**

Western Tree Frog

Material: Male, NGK-Nimba 0016 (Fig. 6F). **Comments:** *Leptopelis occidentalis* is primarily a rainforest treefrog, preferring forests near streams, and

ranging from western Ghana, through Ivory Coast to Liberia (Schiøtz 1967; Rödel et al. 2005; Hillers and Rödel 2007; Hillers et al. 2009; Channing and Rödel 2019). After sunset (1830 h GMT), a male (41.5 mm SUL) with a uniform green dorsum was found perching on a shrub at the edge of a forest clearing along a stream (07°33.121'N, 008°25.036'W; 422 m asl). The species is known from several forests in Ivory Coast (Schiøtz 1967; Rödel and Branch 2002; Ernst and Rödel 2008).

***Leptopelis spiritusnoctis* Rödel, 2007**

Ghostly Tree Frog

Material: Female, NGK-Nimba 0087 (Fig. 6G).

Comments: *Leptopelis spiritusnoctis* inhabits patches of degraded and primary forests, from Sierra Leone to Nigeria (Schiøtz 1967; Rödel 2007; Rödel et al. 2014). During this survey we collected only one female (33.5 mm SUL) in a tree at the edge of a stream (07°33.121'N, 008°25.036'W; 422 m asl).

***Leptopelis viridis* (Günther, 1869)**

Green Tree Frog

Material: One male, NGK-Nimba 0083, and one female, NGK-Nimba 0086 (Fig. 6H). **Comments:** *Leptopelis viridis* is a savannah frog, which is also encountered in herbaceous vegetation from the semi-deciduous forest zone. It ranges across the northern part of sub-Saharan Africa (Schiøtz 1967; Rödel 2000; Channing and Rödel 2019). The species was recorded within grassland at the foot of Mounts Nimba (07°35.453'N, 008°24.957'W; 843 m asl). Additional populations were recorded in the Yéalé village, on shrubs, palm trees, and herbaceous plants (07°31.928'N, 008°25.401'W; 425 m asl). The males measured 32.0–34.0 mm (N = 6), while a single recorded female reached 36.0 mm SUL.

Bufonidae

***Nimbaphrynoides occidentalis* (Angel, 1943)**

Nimba Toad

Material: No voucher. **Comments:** *Nimbaphrynoides occidentalis* is a unique toad, being viviparous and endemic to a very limited range of a total of 4 km² on the ridges of the Mounts Nimba between Liberia, Guinea, and Ivory Coast (Lamotte 1959; Lamotte and Sanchez-Lamotte 1999; Hillers et al. 2008b; Sandberger-Loua et al. 2016, 2017). The toads live in montane grasslands above 1,200 m asl, where they go into dormancy during the dry season (Lamotte 1959; Hillers et al. 2008; Sandberger et al. 2010). *Nimbaphrynoides occidentalis* comprises two subspecies isolated by a forested mountain ridge: the larger *N. occidentalis liberiensis* is restricted to one site in Liberia, while *N. occidentalis occidentalis* occurs in a few sub-populations in Guinea and Ivory Coast (Sandberger et al. 2010). We found *N. occidentalis occidentalis* at 1,235 m asl, on very humid steep slopes in the montane grassland (07°35.555'N, 008°25.788'W;

1,235 m asl). Four juveniles and one female were discovered under rocks. The sizes of the juveniles ranged from 12.0–14.0 mm while the female measured 23.0 mm. The basic dorsal color of the juveniles was dark brown, with a somewhat irregular mixture of light brown and white spots. Their snout, eyelids, and legs were colored light brown. The juveniles showed a pattern typical for adult males (Fig. 7A), whereas the female had a nearly uniform light brown dorsal color (Fig. 7B). The main threat for this species in Ivory Coast is bush fires in the dry season. A detailed assessment of the distribution and population sizes of *N. occidentalis occidentalis* from Ivory Coast is urgently needed.

***Sclerophrys maculata* (Hallowell, 1854)**

Northern Flat-backed Toad

Material: Two males, NGK-Nimba 0043, NGK-Nimba 0051 (Fig. 7C), and one female, NGK-Nimba 0058 (Fig. 7D). **Comments:** *Sclerophrys maculata* is a common toad with flat and granular parotid glands living in the savannah zone and edges of heavily degraded forests (Rödel 2000; Poynton et al. 2016). Toads were found in grassy pastures at the foot of Mounts Nimba (07°35.258'N, 008°25.052'W; 821 m asl), and some females were also observed occasionally together with *S. togoensis* on forest trails (07°32.993'N, 008°24.753'W; 425 m asl). Further records were obtained in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl), mostly along dirt roads in puddles, around houses, or in plantations at swamp edges. The body sizes of two males were 46.0 and 49.0 mm, while females measured 41.5–69.0 mm (N = 5). During the reproductive period, some males exhibited a remarkable yellow color.

***Sclerophrys regularis* (Reuss, 1833)**

Common Toad

Material: Female, NGK-Nimba 0031 (Fig. 7E). **Comments:** *Sclerophrys regularis* has prominent, roundish, and smooth parotid glands. It inhabits a broad range of habitats from moist and dry savannahs to forest margins throughout tropical Africa, most often found around human settlements (Rödel 2000; Channing and Howell 2006). The species was recorded in the rainy season at Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl), where some males called in garbage pits (e.g., Fig. 7F). A female toad measured 118.0 mm, while a male's body size was 102.0 mm.

***Sclerophrys togoensis* (Ahl, 1924)**

Togo Toad

Material: Three males, NGK-Nimba 0004, NGK-Nimba 0028, NGK-Nimba 0029 (Fig. 7G), and one female, NGK-Nimba 0050 (Fig. 7H). **Comments:** This toad has a patchy distribution in primary forests from Togo to Sierra Leone, and mainly breeds in shallow forest streams during the dry season (Rödel and Bangoura 2004; Rödel et al. 2004). Four specimens were found

in different forest patches. The variable color pattern of this species has been described by Rödel and Bangoura (2004), Channing and Rödel (2019), and Gongomin et al. (2019). Diagnostic is the parallel, straight, narrow, and angular parotid glands, running parallel to the side of the body. Two males were encountered in a patch of dense forest crossed by a shallow stream (07°33.440'N, 008°24.657'W; 439 m asl). A female was found together with another male among humid litter on a forest trail (07°32.993'N, 008°24.753'W; 425 m asl). While the female measured 64.0 mm, the SULs of the three males ranged from 40.5–44.5 mm. In Ivory Coast, *S. togoensis* is highly threatened by deforestation (Gongomin et al. 2019).

Conrauidae

***Conraua alleni* (Barbour and Loveridge, 1927)**

Allen's Giant Frog

Material: Two unsexed, NGK-Nimba 0057 (Fig. 8A), NGK-Nimba 0058, and two females, NGK-Nimba 0059 (Fig. 8B), NGK-Nimba 0073. **Comments:** *Conraua alleni* is a highly aquatic frog, which inhabits slow- to fast-flowing forest streams, from lowlands to montane forest areas. Records are known from eastern Guinea and Sierra Leone, through Liberia to western Ivory Coast, with an isolated population occurring in western Ghana (Barbour and Loveridge 1927; Guibé and Lamotte 1958a; Lamotte and Perret 1968; Rödel 2003; Rödel and Bangoura 2004; Channing and Rödel 2019; Rödel and Glos 2019; Schäfer et al. 2019). Some of these populations may comprise cryptic taxa (see Rödel and Branch 2002; Hillers et al. 2008a). We found *C. alleni* populations in streams intersecting forest patches (07°35.258'N, 008°25.052'W; 821 m asl). Other individuals were heard calling in a very impressive torrent stream in mid-elevation forest (07°34.652'N, 008°24.966'W; 716 m asl). The bird-like whistles were heard during day and night, with peaks after sunset (around 1841 h GMT). Additional populations were found at night in pools of a slow running stream with a sandy and rocky bottom. This stream crossed a slightly degraded forest patch dominated by bamboo (07°32.993'N, 008°24.753'W; 425 m asl), where a total of 14 adult frogs were caught. Through palpation of the lower abdomen, two of them were identified as gravid females. Their body size was 52.8–54.0 mm. The remaining 12 frogs ranged from 51.1–55.6 mm but could not be sexed. One adult, kept in captivity for two months, preyed on locusts, ants, spiders, caterpillars, and butterflies that were floating on the water surface. All adult *C. alleni* had a clear interorbital line, however, their back pattern varied from a darker brown with black dots and reddish legs to frogs with orange patches on the darker brown ground. In contrast to other described *C. alleni* (e.g., Channing and Rödel 2019), the venter of our frogs was golden yellow or beige to pinkish, and the thighs had a pink ventral color. The

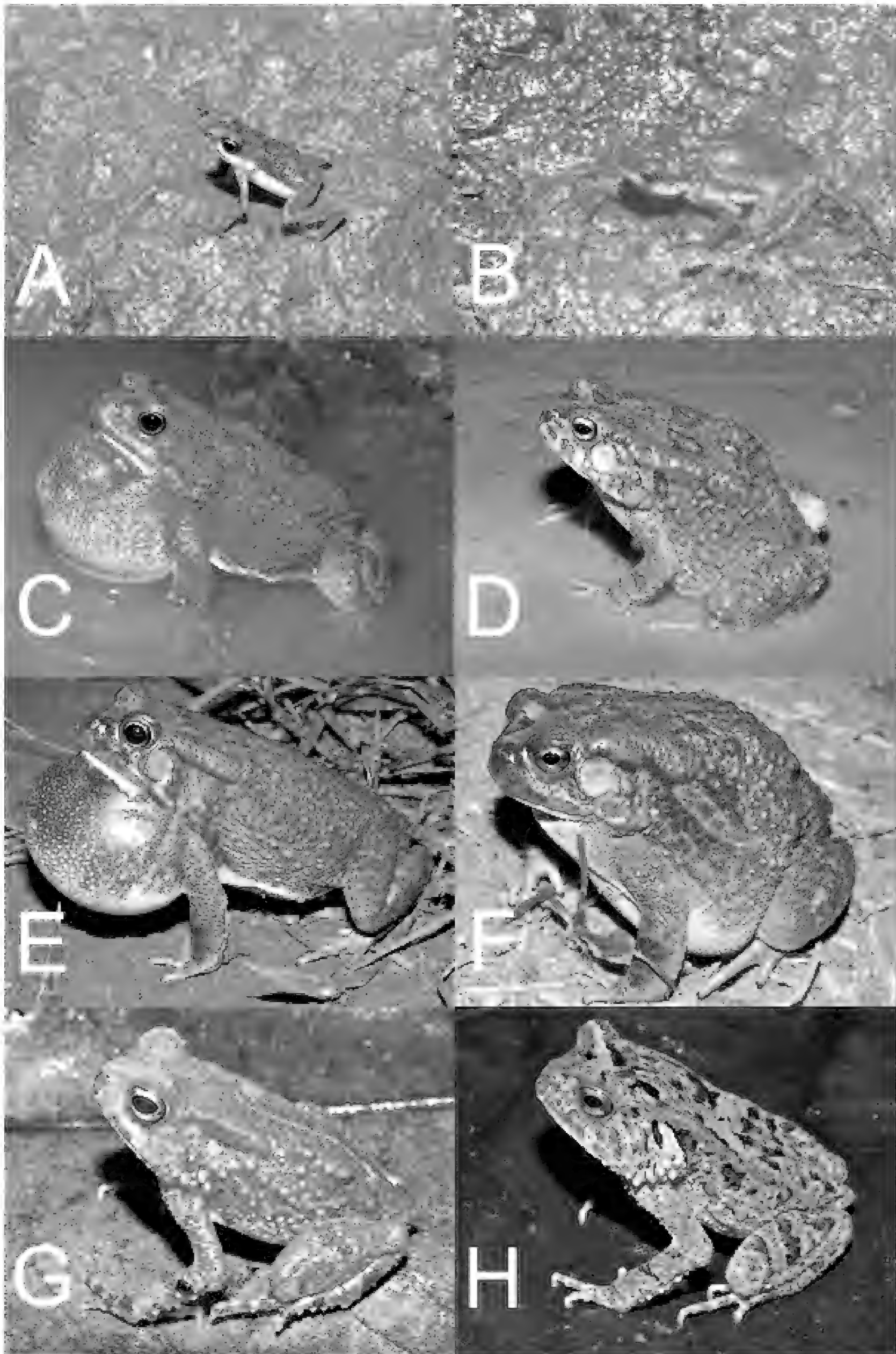


Fig. 7. Bufonids from Mount Nimba Integrated Nature Reserve: *Nimbaphrynoides occidentalis* juvenile (A); *N. occidentalis* female (B); *Sclerophrys maculata* male (C), the yellow color is only exhibited by some males during breeding; *S. maculata* female (D); *S. regularis* male (E); *S. regularis* female (F); *S. togoensis* male (G); *S. togoensis* female (H).

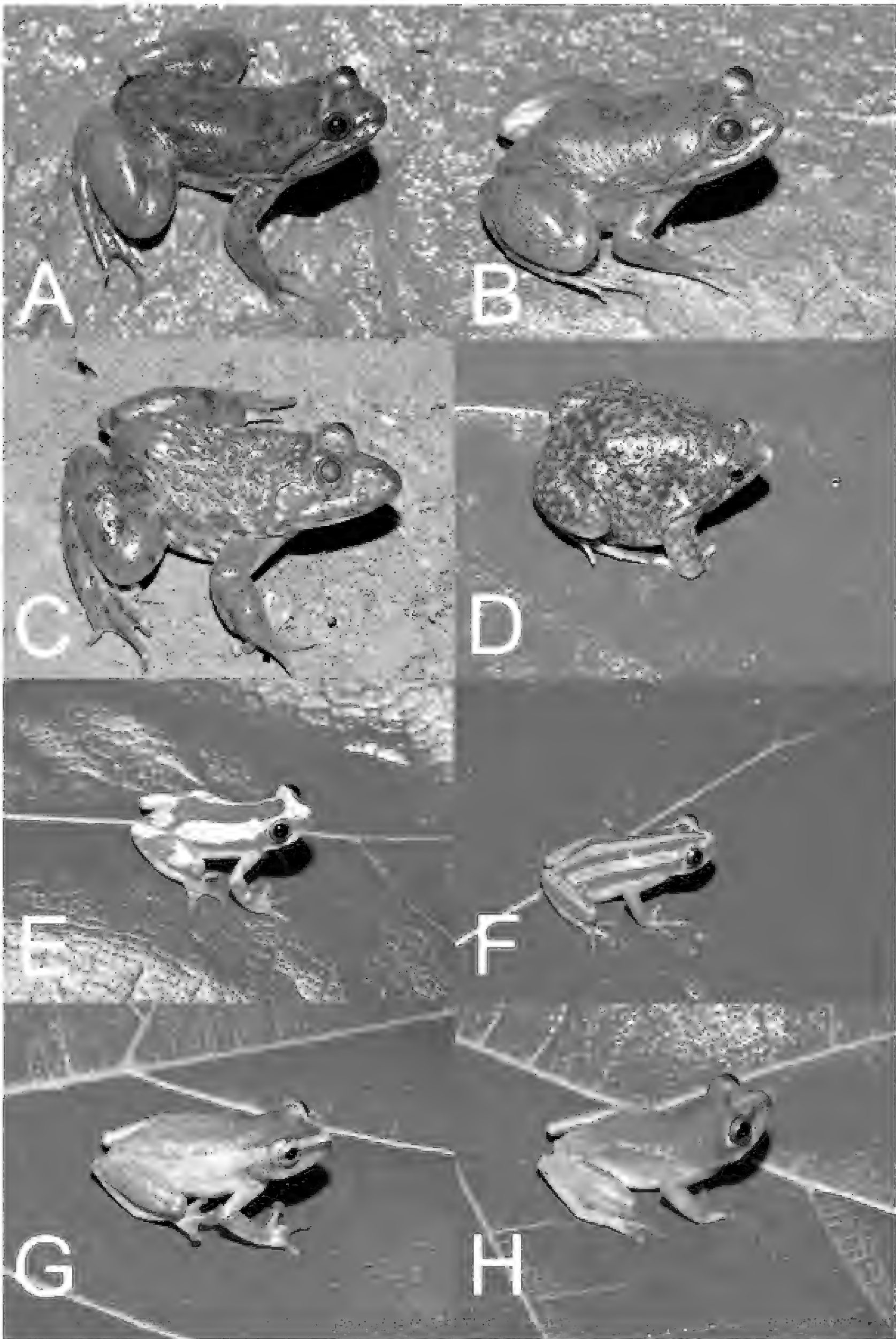


Fig. 8. Conrauid, dicroglossid, hemisotid, and hyperoliids from Mount Nimba Integrated Nature Reserve: *Conraua alleni* (A–B); *Hoplobatrachus occipitalis* (C); *Hemisus marmoratus* (D); *Afrixalus dorsalis* (E); *A. fulvovittatus* (F); *Hyperolius chlorosteus* (G–H).

throat was dark, and pinkish with reddish-brown dots or uniform beige. The taxonomic status of these frogs and the populations from nearby Mount Sangbé National Park (Rödel 2003) should be investigated.

Dicroglossidae

Hoplobatrachus occipitalis (Günther, 1858)

African Tiger Frog

Material: Female, NGK-Nimba 0005 (Fig. 8C).

Comments: *Hoplobatrachus occipitalis* is a large aquatic frog that is widely distributed in savannahs and disturbed forests across tropical Africa (Channing and Rödel 2019). A female was caught at night near a stream within pastures (07°35.453'N, 008°24.957'W; 843 m asl). Males were heard calling at night, concealed in rice paddies in Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). In the rainy season, adult frogs were occasionally collected and eaten by the local populations around the MNINR (Zogbassé et al., unpub. data).

Hemisotidae

Hemissus marmoratus (Peters, 1854)

Marbled Piglet Frog

Material: Two males, NGK-Nimba 0085, NGK-Nimba 0089 (Fig. 8D). **Comments:** *Hemissus marmoratus* is a fossorial frog, very common in the savannah ecoystems of sub-Saharan Africa (Rödel 2000; Channing and Rödel 2019). We found it in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl), among short grasses at puddles, in leaf litter under cocoa and coffee trees, and around a manual hydraulic water pump. The body size of males ranged from 29.0–34.5 mm (N = 4), while females measured between 33.0–50.5 mm (N = 8).

Hyperoliidae

Afrixalus dorsalis (Peters, 1875)

Striped Spiny Reed Frog

Material: Male, NGK-Nimba 0051 (Fig. 8E).

Comments: *Afrixalus dorsalis* is a nocturnal leaf-folding frog, which inhabits a wide range of western African habitats, such as savannah, farmbrush, and swampy areas at forest edges (Schjötz 1967; Rödel 2000; Channing and Rödel 2019). We heard many calling males in rice paddies and in grassy vegetation of swamps, in Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). A male measured 22.0 mm SUL.

Afrixalus fulvovittatus (Cope, 1861)

Banded Spiny Reed Frog

Material: Two females, NGK-Nimba 0066, NGK-Nimba 0067 (Fig. 8F). **Comments:** *Afrixalus fulvovittatus* can be easily recognized by its characteristic reddish-brown dorsal surface with three light longitudinal stripes joining on the tip of the snout. The delicate reddish-brown line

in the middle of each light stripe distinguishes it from the similar looking *A. vittiger* (Pickersgill 2007). This nocturnal species prefers the heavily degraded habitats of the forest zone (Schjötz 1967; Rödel and Glos 2019). In the Yéalé village, the species was found in rice paddies and grassy swamps (07°31.928'N, 008°25.401'W; 425 m asl). The SULs of two females were 19.8–21.0 mm, thus they were below the described size for *A. fulvovittatus* (Schjötz 1967).

Hyperolius chlorosteus (Boulenger, 1915)

Large Green Reed Frog

Material: Three males, NGK-Nimba 0075 (Fig. 8G), NGK-Nimba 0076 (Fig. 8H), NGK-Nimba 0088.

Comments: *Hyperolius chlorosteus* is common along streams in pristine forest from western Ivory Coast to Sierra Leone (Schjötz 1967; Channing and Rödel 2019). In Ivory Coast, it was reported from the rainforest zone, i.e., the Taï National Park (e.g., Schjötz 1967; Rödel et al. 2002), as well as from the edge of the forest zone in the Mount Sangbé National Park (Rödel 2003). Records from Mount Péko National Park (Rödel and Ernst 2003) and the Haute Dodo and Cavally forests (Rödel and Branch 2002) may no longer exist. Thus, our records of *H. chlorosteus* from Mounts Nimba, confirming the records by Schjötz (1967), show that the species prevailed, at least here, through the past 50 years. The species was frequently recorded at night along streams in the primary forest. After a heavy rainfall, a vast number of males (N > 50) were heard calling from high up in tall trees along a torrent stream (07°34.652'N, 008°24.966'W; 716 m asl). Five males were captured, and their body sizes ranged from 33.2–37.0 mm. They showed some variation of their back coloration, however, within the range known for the species (compare Schjötz 1967; Channing and Rödel 2019). We found one male in sympatry with *L. macrotis* in a degraded forest during the rainy season (07°31.932'N, 008°25.508'W; 387 m asl), perched up at approximately 1.80 m above the ground, close to a large stream. Most males, however, called from much higher sites.

Hyperolius concolor (Hallowell, 1844)

Uniform Reed Frog

Material: One female, NGK-Nimba 0011 (Fig. 9A), and two males, NGK-Nimba 0012 (Fig. 9B), NGK-Nimba 0020. **Comments:** *Hyperolius concolor* is one of the most common West African frogs, widespread in a range of habitats from savannahs and farmbrush to degraded and gallery forests (Schjötz 1967; Rödel 2000). It even has been reported from urban sites (Kouamé et al. 2015). Calling males were abundant in rice paddies and grass-covered edges of ponds (07°31.928'N, 008°25.401'W; 425 m asl). The species is dichromatic (Portik et al. 2019), with females exhibiting a uniform light yellowish-green back with reddish toe discs (SUL: 32.0–33.0 mm, N = 2); males in contrast are brownish, often with some

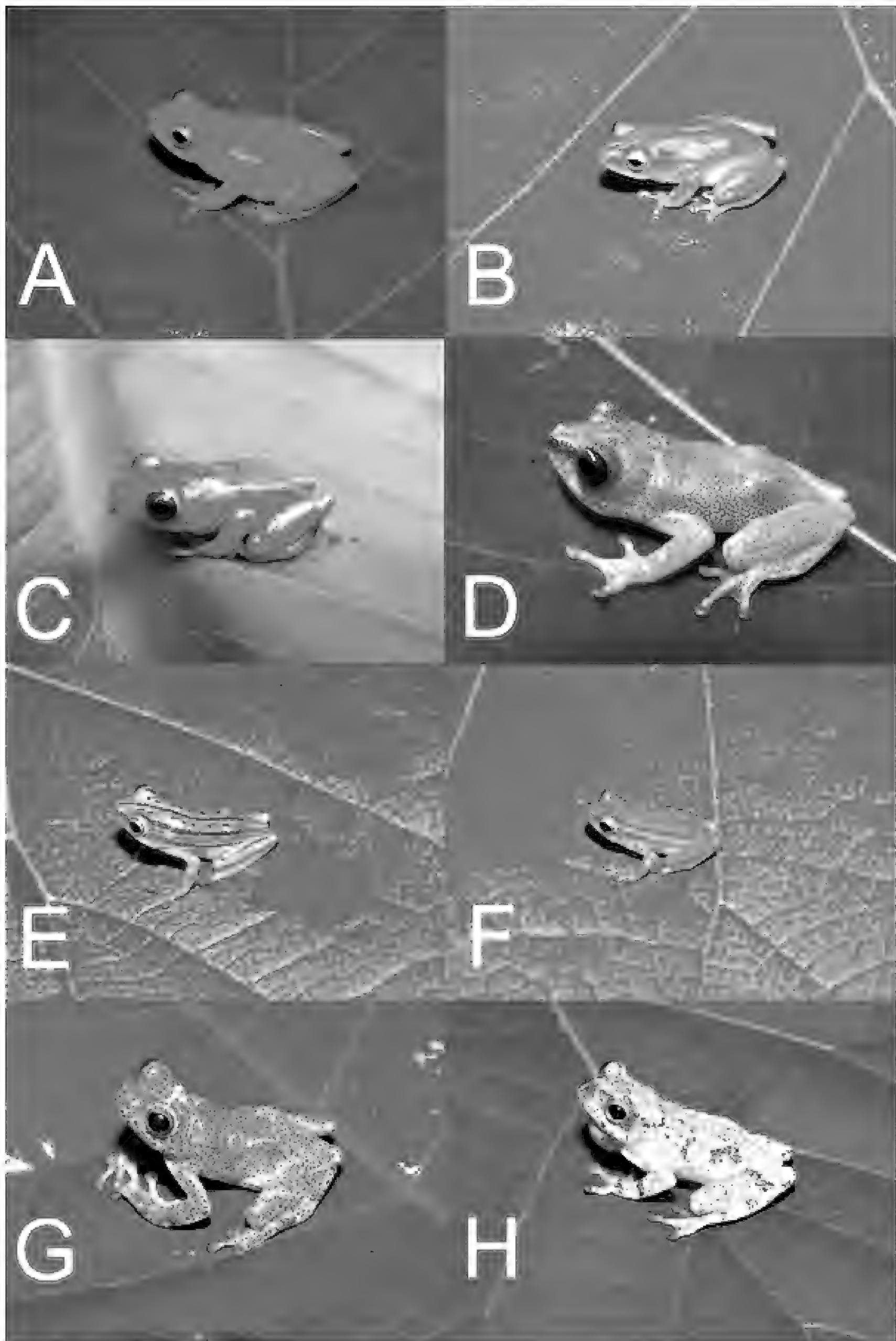


Fig. 9. Hyperoliid frogs from Mount Nimba Integrated Nature Reserve: *Hyperolius concolor* female (A); *H. concolor* male (B); *H. fusciventris fusciventris* male (C); *H. guttulatus* female (D); *H. lamottei* female (E); *H. lamottei* male (F); *H. nimbae* female (G); *H. nimbae* male (H).

dark patterns between the eyes and on the back (SUL: 23.5–25.5 mm, N = 5).

***Hyperolius fusciventris fusciventris* Peters, 1876**

Dark-bellied Reed Frog

Material: Male, NGK-Nimba 0077 (Fig. 9C).

Comments: *Hyperolius fusciventris fusciventris* occurs from western Ivory Coast into neighboring Liberia and Guinea in farmbush, heavily degraded forests, and occasionally in gallery forests within humid savannah (Schjötz 1967). We encountered the species in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl), in an open but densely vegetated area close to swamps. The dorsal color varied from uniform brownish over light green to dense green. Some individuals with greyish-blue eyes exhibited a uniform yellow dorsal color. The belly of females was either dark or light grey. All males had a lighter belly. The male SULs ranged from 23.5–25.0 (N = 7), females reached 26.5–27.0 mm (N = 3).

***Hyperolius guttulatus* Günther, 1858**

Spotted Reed Frog

Material: Female, NGK-Nimba 0052 (Fig. 9D).

Comments: *Hyperolius guttulatus* lives in the humid savannah zone and clearings within rainforests (Schjötz 1967; Rödel 2000; Asseman et al. 2006; Kouamé et al. 2015). The species usually reproduces in larger, permanent ponds with floating vegetation (Schjötz 1967; Kouamé et al. 2015). We found five males calling at night between rice paddies around the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). A female measured 37.0 mm.

***Hyperolius lamottei* Laurent, 1958**

Lamotte's Reed Frog

Material: One female, NGK-Nimba 0074 (Fig. 9E), and two males, NGK-Nimba 0081 (Fig. 9F), NGK-Nimba 0082. **Comments:** *Hyperolius lamottei* is a savannah frog with a patchy distribution, preferring low grass habitats, often in higher altitude, e.g., granite inselbergs in central-southern Ivory Coast, Liberia, Guinea, Sierra Leone to Senegal (Arnoult and Lamotte 1958; Lamotte 1969, 1971; Schjötz 1967; Rödel et al. 2004). Recently, it was reported for the first time from Burkina Faso (Ayoro et al. 2020). In Ivory Coast, the species was recorded from the Lamto Faunal Reserve (Schjötz 1967) and the Mount Péko National Park (Rödel and Ernst 2003). However, more recently Adeba et al. (2010) failed to re-detect the species in Lamto. We found *H. lamottei* in large numbers in grassy montane pasture (07°35.258'N, 008°25.052'W; 821 m asl). The species was only active during the rainy season, when males and females became active after sunset. They spent the night perching on high grasses which covered a flooded iron-oxide quartzite ground. During the daytime all frogs hid within the dense herbaceous vegetation. Body size of males ranged from 17.5–19.0 mm (N = 4), females measured 21.5–23.5 mm

(N = 3). Color pattern was variable, but within the range described by Schjötz (1967).

***Hyperolius nimbae* Laurent, 1958**

Nimba Reed Frog

Material: One female, NGK-Nimba 0070 (Fig. 9G),

and two males, NGK-Nimba 0078, NGK-Nimba 0079 (Fig. 9H). **Comments:** *Hyperolius nimbae* is a farmbush frog, endemic to the eastern foothills of Mounts Nimba (Schjötz 1967). After 47 years, this species was only recently rediscovered by Kouamé et al. (2016), reporting small populations from four villages (Dagbonpleu, Danipleu, Kouan-Houlé, and Zéalé) within the formerly known range. An even more recent re-investigation in these villages failed to confirm the species, and its known habitats had been destroyed due to road expansions, development, and urbanization (Gongomin et al., unpub. data). However, during our study, we encountered a large number of *H. nimbae* males in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). The habitat was within a plantation of cocoa and coffee that edged a large and deep pond, which exceeded 100 x 70 m. There, we observed 15 males at night between broad leaved, evergreen trees of cocoa and coffee, while only one female was seen perched between the leaves of a palm tree. The males ranged from 30.0–35.5 mm (N = 15), the female measured 34.1 mm. Males varied considerably in color and also showed some differences in pattern compared to the female. However, both sexes matched earlier descriptions by Schjötz (1967).

***Hyperolius picturatus* Peters, 1875**

Painted Reed Frog

Material: One female, NGK-Nimba 0104 (Fig. 10A),

and one male, NGK-Nimba 0105 (Fig. 10B). **Comments:** *Hyperolius picturatus* inhabits farmland and forest areas in various state of degradation, from central Ghana to Sierra Leone (Schjötz 1967; Rödel 2000; Channing and Rödel 2019). We found the species in an agricultural area of the Yéalé village. The basic dorsal color of males (28.0–31.5 mm, N = 4) was brownish with two light, broad dorsolateral stripes, while the venter, including gular glands, was entirely yellow. A female (35.5 mm) had yellow, broad dorsolateral stripes with some small yellow spots on its black chin. Its venter likewise was bright yellow. This widespread taxon shows some color variation across its range and may comprise two species (Schjötz 1967; Rödel and Branch 2002; Rödel and Glos 2019).

***Hyperolius soror* (Chabanaud, 1921)**

Soror Reed Frog

Material: One female, NGK-Nimba 0125 (Fig. 10C),

two males, NGK-Nimba 0126 (Fig. 10D), NGK-Nimba 0127. **Comments:** We heard over a dozen *H. soror* males calling during the rainy season in a dense grassy swamp, edging forest (07°32.993'N, 008°24.753'W; 425 m asl).

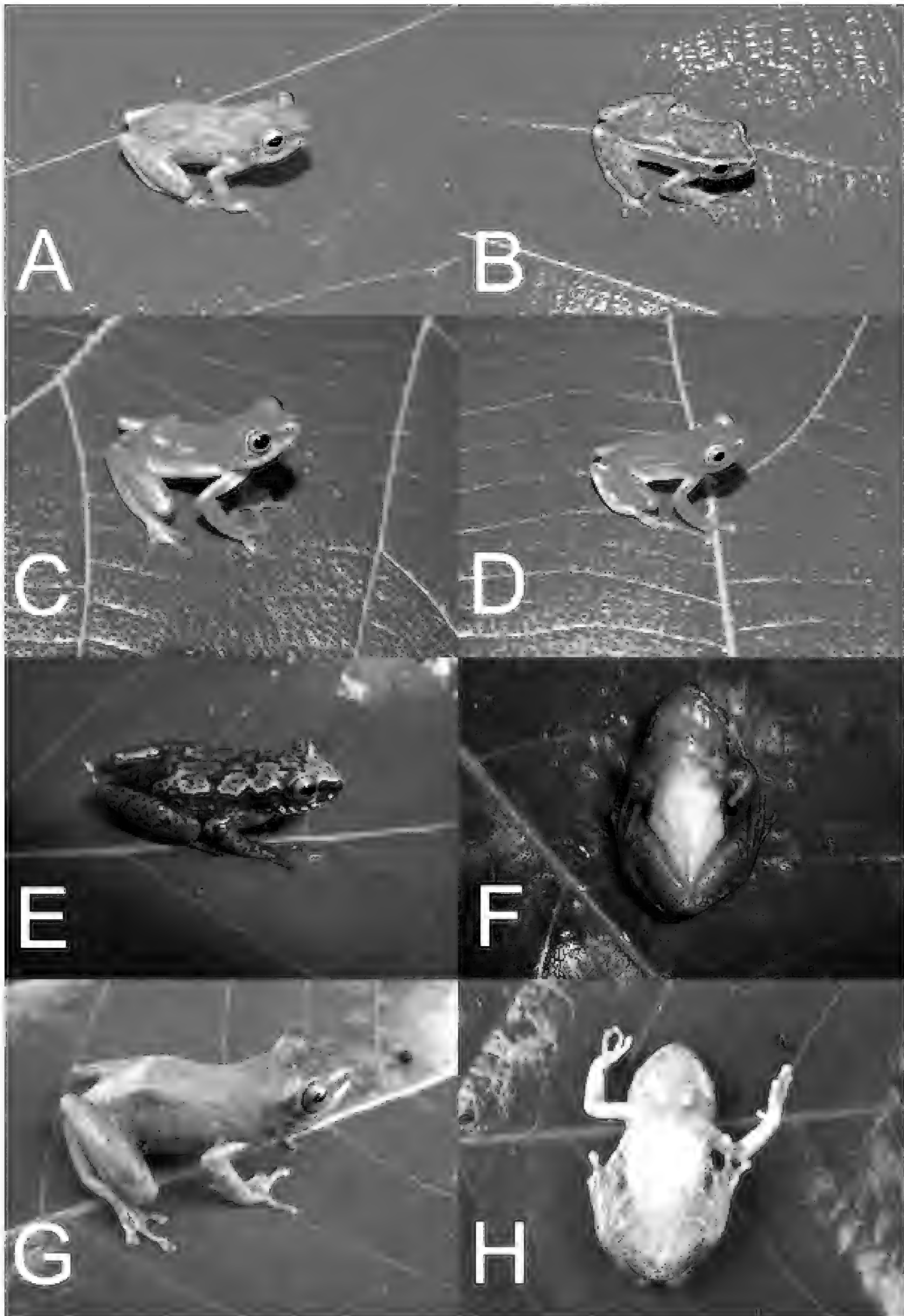


Fig. 10. Hyperoliid frogs from Mount Nimba Integrated Nature Reserve: *Hyperolius picturatus* female (A); *H. picturatus* male (B); *H. soror* female (C); *H. soror* male (D); *H. cf. sylvaticus* male (E); *H. cf. sylvaticus* male in ventral view (F); *H. sp.* male (NGK-Nimba 0068) (G); *H. sp.* male (NGK-Nimba 0068) in ventral view (H).

However, only one female and two males were caught there. The species is sexually dimorphic. The female (25.1 mm SUL) had a light green back, with diffuse, minute, reddish-brown spots, red lateral markings, a red stripe from snout to tip of eye, bluish-grey iris, and toes and fingers, including webbing, were faintly red with green tips. Its ventral surface was transparent bluish green. In contrast, both males (SUL 19.1 and 21.1 mm) had a golden iris, a dark red canthal stripe, green dorsum with diffuse, minute, reddish-brown spots, light dorsolateral stripes, and green toes and fingers.

***Hyperolius cf. sylvaticus* Schiøtz, 1967**

Forest Reed Frog

Material: Male, NGK-Nimba 0108 (Fig. 10E–F).

Comments: *Hyperolius cf. sylvaticus* was recorded in an open area in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). However, *H. sylvaticus* is known to be a forest species (Schiøtz 1967; Rödel and Branch 2002; Ernst and Rödel 2008), thus it might just as well be a member of the *Hyperolius picturatus*-complex.

***Hyperolius* sp.**

Material: Male, NGK-Nimba 0068 (Fig. 10G–H).

Comments: Two *Hyperolius* sp. were recorded in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl), in a swampy area with a shallow creek, dense herbaceous formations, and few shrubs and trees. A male (26.4 mm) possessed a uniform greyish-brown dorsal color; the throat was dull blue; the anterior part of the belly was white, the posterior part greenish to blueish. The ventral surfaces of limbs were greenish; the discs of toes and fingers were reddish. The gular gland was indistinct and smooth. So far, we cannot assign these frogs to any West African *Hyperolius* species (e.g., Schiøtz 1967; Channing and Rödel 2019). Molecular and acoustic data are required in order to resolve the taxonomic status of this reedfrog.

***Kassina cochranæ* (Loveridge, 1941)**

Cochran's Running Frog

Material: Four males, NGK-Nimba 0139, NGK-Nimba 0140, NGK-Nimba 0141 (Fig. 11A), NGK-Nimba 0142.

Comments: *Kassina cochranæ* is an arboreal forest and farmbush dweller, ranging from the rainforest edge into the moist savannah zone from western Ivory Coast to eastern Sierra Leone (Schiøtz 1967; Rödel et al. 2002). During the rainy season, we heard a vast number of males calling concealed in dense vegetation, close to a grassy swamp (habitat C: 07°32.993'N, 008°24.753'W; 425 m asl). Four males measured 34.0–36.5 mm. In the Yéalé village, a *K. cochranæ* metamorph was found by dip-netting in a deep pond in dense farmbush vegetation. At night, adult males were heard calling at the same site between inaccessible dense vegetation, edging a swamp (07°31.928'N, 008°25.401'W; 425 m asl).

Odontobatrachidae

***Odontobatrachus arndti* Barej, Schmitz, Penner, Doumbia, Sandberger-Loua, Emmrich, Adeba, and Rödel, 2015**

Arndt's Toothed Frog

Material: Three females, NGK-Nimba 0244, NGK-Nimba 0245, NGK-Nimba 0246, and two males, NGK-Nimba 0247 (Fig. 11A), NGK-Nimba 0248. **Comments:** *Odontobatrachus arndti* is a torrent-frog living in primary and slightly degraded forests, known from Mount Sangbé and Mounts Nimba (Barej et al. 2015; Channing and Rödel 2019). We found a few populations of *O. arndti* along cascades of streams in forested ravines edged by savannah (07°35.233'N, 008°25.190'W; 847 m asl). These frogs were found to be very abundant along a very torrent stream (07°34.652'N, 008°24.966'W; 716 m asl). In a lower part of the forest, an additional site was along a wide torrent stream with a gravel bottom and blocks of granite rock (07°33.121'N, 008°25.036'W; 422 m asl). The recorded males exhibited huge bright orange femoral glands. They measured 45.1–52.5 mm (N = 8); the female SUL ranged from 43.5–60.5 mm (N = 10), thus the sizes of both sexes are within the known range of the species (Barej et al. 2015). At all sites, the majority of frogs were close to the rocky streams, however, a few females perched on trees close to the streams. These records are the second for Ivory Coast.

Phrynobatrachidae

***Phrynobatrachus alleni* Parker, 1936**

Allen's Puddle Frog

Material: Male, NGK-Nimba 0010 (Fig. 11C).

Comments: During the rainy season, we found a yellow *Phrynobatrachus alleni* male (18.5 mm) in breeding condition, among leaf litter on the forest floor, in a patch of dense forest, crossed by a small stream (07°32.993'N, 008°24.753'W; 425 m asl). Rödel (2003) reported from nearby Mount Sangbé that breeding *P. alleni* became completely yellow. The yellow color may disappear within minutes when the frogs are disturbed. In Taï National Park, breeding *P. alleni* males were never observed to be completely yellow (M.-O. Rödel, unpub. data).

***Phrynobatrachus annulatus* Perret, 1966**

Ringed Puddle Frog

Material: Two females, NGK-Nimba 0091 (Fig. 11D), NGK-Nimba 0094.

Comments: *Phrynobatrachus annulatus* is a forest-dwelling leaf litter frog, which has a patchy distribution in forests from south-eastern Guinea, eastern Liberia, western Ivory Coast, and western Ghana (Ernst and Rödel 2006; Hillers and Rödel 2007; Rödel et al. 2005; Rödel and Glos 2019). In Ivory Coast, the species was reported from Taï National Park (e.g., Ernst and Rödel 2006; Hillers et al. 2008c), and the Mabi-Yaya

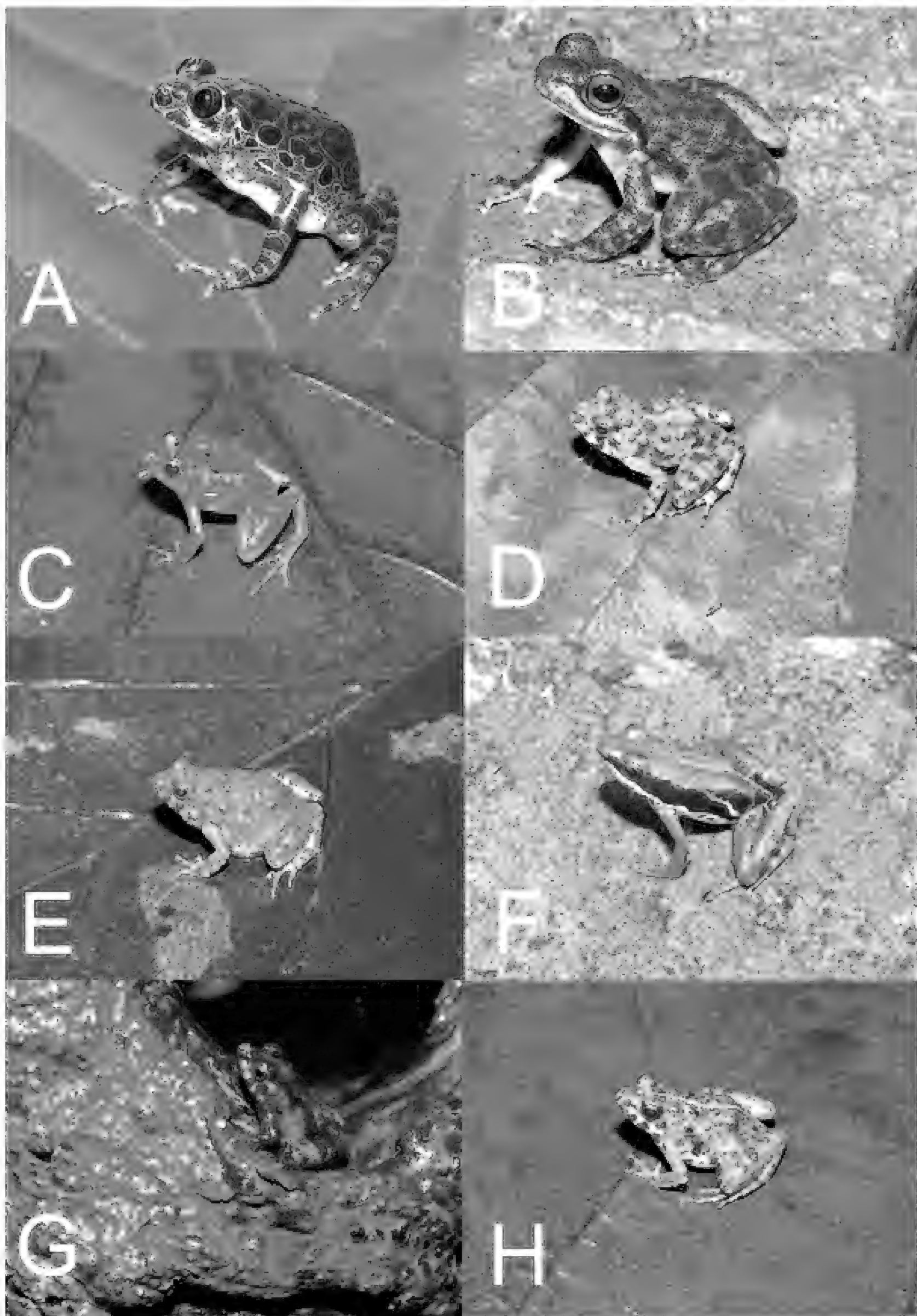


Fig. 11. Hyperoliid, odontobatrachid, and phrynobatrachid frogs from Mount Nimba Integrated Nature Reserve: *Kassina cochranae* male (A); *Odontobatrachus arndti* male (B); *Phrynobatrachus alleni* male (C); *P. annulatus* male (D); *P. francisci* female (E); *P. fraterculus* female (F); *P. guineensis* male (G); *P. guttuerosus* female (H).

Forest Reserve (Gongomin et al. 2019). We found two young females of *P. annulatus* (14.0 and 20.2 mm) in a site with high canopy forest on the slopes of a large granite inselberg. The dry forest ground was covered with multiple layers of leaf litter, but the undergrowth was sparse (07°34.364'N, 008°24.746'W; 643 m asl). Drier parts of the forest along slopes of inselbergs also comprise the usual habitat where this species was recorded in Taï National Park (M.-O. Rödel, unpub. data).

***Phrynobatrachus francisci* Boulenger, 1912**

Francisc's Puddle Frog

Material: Two females, NGK-Nimba 0092 (Fig. 11E), NGK-Nimba 0093. **Comments:** *Phrynobatrachus francisci* occurs in moist Guinea savannah and drier Sudanese savannah, from Senegal to Nigeria (Rödel 2000; Channing and Rödel 2019). We found the species in the rainy season, among dense herbaceous vegetation at the edge of a puddle (07°31.928'N, 008°25.401'W; 425 m asl). Two females (20.5–22.0 mm) were caught in the Yéalé village during late afternoon (1618 h GMT).

***Phrynobatrachus fraterculus* (Chabanaud, 1921)**

Brother's Puddle Frog

Material: Female, NGK-Nimba 072 (Fig. 11F). **Comments:** *Phrynobatrachus fraterculus* is known to inhabit degraded forest and forest edges in the western part of the Upper Guinea forest region (Guibé and Lamotte 1963; Rödel and Bangoura 2004; Rödel and Glos 2019). A female (24.0 mm) was found in leaf litter near a shallow creek in a small clearing (07°33.121'N, 008°25.036'W; 422 m asl). In Ivory Coast, the species had been recorded previously in the Taï National Park (Ernst and Rödel 2006; Hillers et al. 2008c).

***Phrynobatrachus guineensis* Guibé and Lamotte, 1962**

Guinea Puddle Frog

Material: Male, NGK-Nimba 0034 (Fig. 11G). **Comments:** *Phrynobatrachus guineensis* is the only known West African member of its genus that uses water-filled tree holes as breeding sites (Rödel 1998; Rödel et al. 2004; Rudolf and Rödel 2007). A breeding male (15.5 mm) was found in a water-filled tree hole in a patch of dense forest (07°34.696'N, 008°25.015'W; 717 m asl).

***Phrynobatrachus gutturosus* (Chabanaud, 1921)**

Guttural Puddle Frog

Material: Two females, NGK-Nimba 0095 (Fig. 11H), NGK-Nimba 0096, and two males, NGK-Nimba 0097, NGK-Nimba 0098. **Comments:** A complex of cryptic West African puddle frogs is currently known under the name *Phrynobatrachus gutturosus* (Rödel 2000; Zimkus et al. 2010). One species of that complex, *P. afixabirago*, has been recently described from southern Ghana (Ofori-Boateng et al. 2018). Frogs from this complex became known from primary rainforest to dry savannah habitats

(Rödel 2000; Rödel and Spieler 2000; Ernst and Rödel 2006; Nago et al. 2006; Hillers et al. 2008c), and their taxonomic status requires further research. We found *P. gutturosus* among leaf litter in a cocoa and coffee plantation (07°31.928'N, 008°25.401'W; 425 m asl). The plantation comprised a large pond and was used by people from the Yéalé village to grow rice. Numerous individuals of *P. gutturosus* were seen after sunset (1830 h GMT). Two females measured 18.5 and 20.0 mm.

***Phrynobatrachus latifrons* Ahl, 1924**

Savannah Puddle Frog

Material: One female, NGK-Nimba 0064 (Fig. 12A), and one male, NGK-Nimba 0065 (Fig. 12B). **Comments:** *Phrynobatrachus latifrons* is a very common and widespread, semi-aquatic West African puddle frog, living in savannah and heavily degraded rainforest habitats (Rödel 1995 [there erroneously termed *P. francisci*], 2000; Kouamé et al. 2018). The species was abundant in the Yéalé village. In particular, we heard males calling between densely vegetated parts of swamps and paddy fields (07°31.928'N, 008°25.401'W; 425 m asl). An adult female with a broad green back and a light vertebral line exhibited an unusual thin, light longitudinal line on upper surface of the tibia (22.0 mm). A uniform brown frog (18.1 mm) exhibited the bright yellow throat, typical for adult males.

***Phrynobatrachus liberiensis* Barbour and Loveridge, 1927**

Liberian Puddle Frog

Material: Male, NGK-Nimba 0071 (Fig. 12C). **Comments:** *Phrynobatrachus liberiensis* is generally found along swamps and shallow streams in primary forests (Rödel and Branch 2002; Kouamé et al. 2018). Many males were heard calling, being well concealed sitting on the banks of a shallow stream in a swampy patch of dense forest (07°32.993'N, 008°24.753'W; 425 m asl). A male (27.0 mm) and a young female (26.0 mm) were caught.

***Phrynobatrachus natalensis* (Smith, 1849)**

Natal Puddle Frog

Material: Two males, NGK-Nimba 0032 (Fig. 12D), NGK-Nimba 0033, and two females, NGK-Nimba 0035, NGK-Nimba 0036 (Fig. 12E). **Comments:** *Phrynobatrachus natalensis* as currently defined (Channing and Rödel 2019) comprise several cryptic species widespread throughout the savannah areas of sub-Saharan Africa (Zimkus et al. 2010). We encountered the species in the Yéalé village, near road puddles in dense vegetation (07°31.928'N, 008°25.401'W; 425 m asl). Other active males were found at night between tufts of ornamental plants around houses after heavy rainfalls. Adult males were uniform brown (26.0–28.1 mm; N = 6) and had black throats with folds, while adult females (27.8–33.5 mm; N = 8) had white, mottled

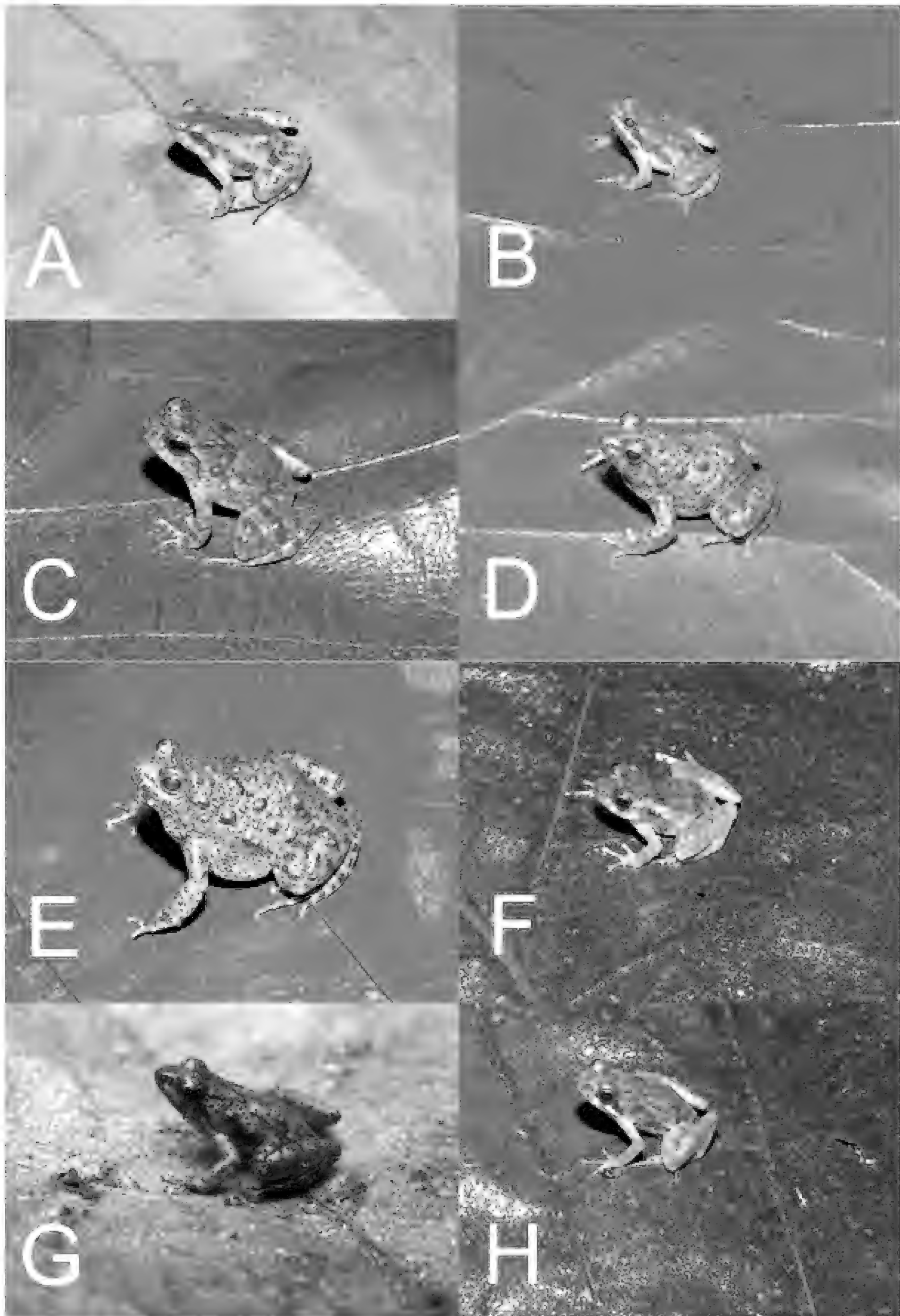


Fig. 12. Phrynobatrachid frogs from Mount Nimba Integrated Nature Reserve: *Phrynobatrachus latifrons* female (A); *P. latifrons* male (B); *P. liberiensis* male (C); *P. natalensis* male (D); *P. natalensis* female (E); *P. phyllophilus* male (F); *P. tokba* female (G); *P. tokba* male (H).

brown or greyish-black throats. One female exhibited an exceptionally conspicuous greyish-brown back with green spots and a green interorbital line; other females being uniform brown. Some frogs reproduced in a large pond within dense vegetation. Four clutches comprising, 938, 1021, 1265, and 1501 small reddish-brown eggs, were floating on the water surface. Mean egg diameter was 0.9 mm (± 0.1 mm; $N = 20$). Clutch sizes therefore seem to be larger in West African, compared to southern African, populations (compare values in Rödel 2000).

***Phrynobatrachus phyllophilus* Rödel and Ernst, 2002**
Leaf-loving Puddle Frog

Material: Male, NGK-Nimba 0037 (Fig. 12F). **Comments:** *Phrynobatrachus phyllophilus* prefers patches of swampy primary forest from eastern Ivory Coast to Sierra Leone (Rödel and Ernst 2002a; Ernst and Rödel 2006; Kouamé et al. 2008, 2014, 2018; Channing and Rödel 2019). We found only one male (15.0 mm) during the rainy season. It was concealed among dense leaf litter, in a patch of dense forest, intersected by a small stream (07°32.993'N, 008°24.753'W; 425 m asl).

***Phrynobatrachus tokba* (Chabanaud, 1921)**
Tokba Puddle Frog

Material: Female, NGK-Nimba 0038 (Fig. 12G). **Comments:** *Phrynobatrachus tokba* occurs in primary to degraded forests, and montane grassland, from western Guinea to Ghana (Guibé and Lamotte 1963; Rödel et al. 2004, 2005; Kouamé et al. 2018; Channing and Rödel 2019). This species reproduces terrestrially, by depositing clutches in moist leaves, and has non-feeding, non-hatching tadpoles (Rödel and Ernst 2002b). A large number of *P. tokba* males called in the drier part of the forest. A brown female measured 18.0 mm. Further populations were detected in moist savannah adjacent to forest, and even in sympatry with *Nimbaphrynoides occidentalis* up to 1,235 m asl in montane grasslands (07°35.555'N, 008°25.788'W; Fig. 12H).

Pipidae

***Xenopus tropicalis* (Gray, 1864)**
Tropical Clawed Frog

Material: Two females, NGK-Nimba 0001 (Fig. 13A), NGK-Nimba 0002, and two males, NGK-Nimba 0003, NGK-Nimba 0006. **Comments:** This pipid lives in forests, degraded forests, and gallery forests in humid savannahs from Senegal to western Cameroon (Rödel 2000). The species was seen in flooded paddy fields in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). In the dry season, frogs were easily caught in patches of the same shallow swamps. Some juvenile frogs measured 21.5–30.0 mm ($N = 5$), adult males reached 32.4–42.5 mm ($N = 5$), and adult females ranged from 48.3–53.3 mm ($N = 4$).

Ptychadenidae

***Ptychadena arnei* Perret, 1997**

Schiøtz's Grass Frog

Material: Male, NGK-Nimba 0053 (Fig. 13C). **Comments:** *Ptychadena arnei* is a poorly studied frog occurring in humid savannahs, secondary forests, and gallery forests, from southern Senegal to central Ivory Coast (Channing and Rödel 2019). Only two females (43.5 and 45.5 mm) and two males (39.5 and 40.5 mm) were recorded at night in the Yéalé village, sitting at the edge of a road puddle that intersected a heavily degraded forest. The basic color of their back was brown to grey with a light triangle on the snout. *Ptychadena oxyrhynchus*, which often have a pale snout as well, have much longer legs (see e.g., Fig. 13F). The *P. arnei* specimens had short dorsolateral folds and possessed distinct sacral folds. They had dark to pale crossbars on the legs and lacked external metatarsal tubercles. A female (Fig. 13B) exhibited a fine yellow vertebral line. A reddish to yellow longitudinal line on the tibia was broad towards the heel, but narrow towards the knee. The upper part of flanks was reddish, while the lower part was grey with black spots. The ventral surface ranged from whitish through beige to yellow. The species is known by its unique advertisement calls, which consist of a long succession of short double calls (Channing and Rödel 2019). In paddy fields around Daloa, western-central Ivory Coast, frogs that were morphologically identical emitted such calls (Kouamé et al., unpub. data).

***Ptychadena bibroni* (Hallowell, 1845)**

Bibron's Grass Frog

Material: One female, NGK-Nimba 0104 (Fig. 13D), and one male, NGK-Nimba 0105. **Comments:** We found *P. bibroni* in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl) along road puddles during the rainy season, and in cocoa and coffee plantations during the dry season. This frog is known from humid savannahs, but was also reported from dry savannahs and open degraded forests (Rödel 2000; Channing and Rödel 2019). The body size of males ranged from 39.0–46.0 mm ($N = 6$), while females reached 46.5–57.0 mm ($N = 7$).

***Ptychadena longirostris* (Peters, 1870)**

Snouted Grass Frog

Material: Female, NGK-Nimba 0039 (Fig. 13E). **Comments:** *Ptychadena longirostris* was found along a forest trail with puddles of various sizes (07°32.993'N, 008°24.753'W; 425 m asl). They had a yellowish back with an ill-defined darker lateral band, stretching from the nares through eyes, tympanum, and flanks to the groin. The size of males ranged from 43.0–46.0 mm ($N = 4$); two females measured 50.0 and 52.5 mm ($N = 2$). This West African species is known to breed in puddles along forest roads (Guibé and Lamotte 1954; Rödel

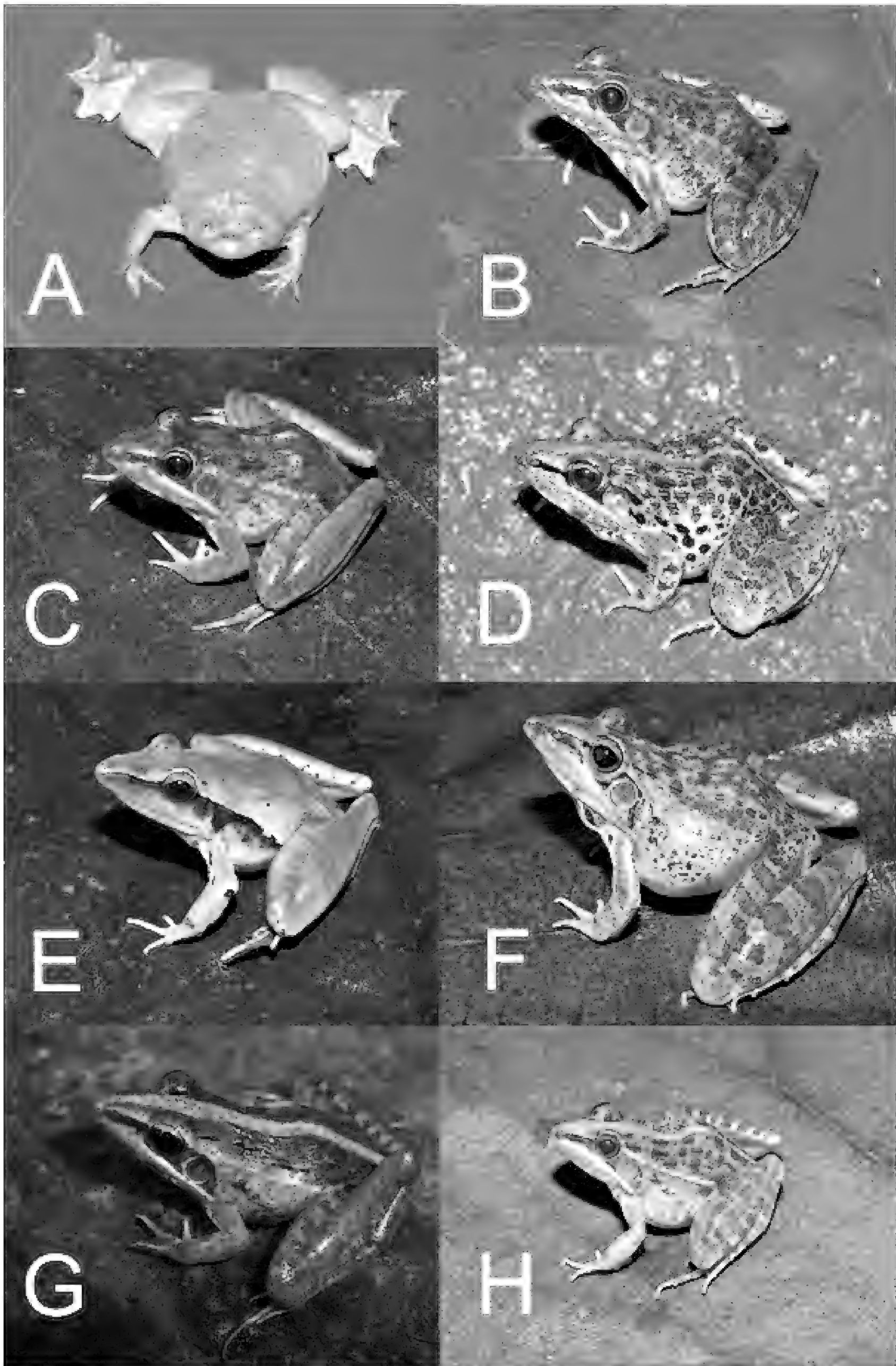


Fig. 13. Pipid and ptychadenid frogs from Mount Nimba Integrated Nature Reserve: *Xenopus tropicalis* female (A); *Ptychadena arnei* female (B); *P. arnei* male (C); *P. bibroni* male (D); *P. longirostris* male (E); *P. oxyrhynchus* male (F); *P. pujoli* male (G); *P. pumilio* female (H).

2000). It preys on various insects and occasionally even aquatic food items (Konan et al. 2016).

***Ptychadena oxyrhynchus* (Smith, 1849)**

Sharp-nosed Grass Frog

Material: Two females, NGK-Nimba 0040, NGK-Nimba 0041, and one male, NGK-Nimba 0042 (Fig. 13F). **Comments:** *Ptychadena oxyrhynchus* is a large frog with extremely robust and long hind legs. It occurs in savannahs and edges of the forest zone across sub-Saharan Africa (Rödel 2000; Channing and Rödel 2019). During the rainy season, the species was found in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl), along dirt roads with temporary water bodies of different sizes. The species survives the dry season in humid parts of rice paddies. In this season, rice is harvested and we saw the frogs in vast numbers. The sizes of two females were 59.0 and 64.8 mm, while a male measured 52.0 mm.

***Ptychadena pujoli* (Lamotte and Ohler, 1997)**

Pujol's Grass Frog

Material: Male, NGK-Nimba 0045 (Fig. 13G). **Comments:** The biology of *Ptychadena pujoli* is very insufficiently known. It seems to occur in savannah swamps and grassland habitats from eastern Sierra Leone, through the Upper Guinea highlands, to western Ivory Coast (Lamotte and Ohler 1997; Channing and Rödel 2019). After a heavy rainfall, some migrating individuals were found among short grasses near houses in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). A male (48.5 mm SUL) with a brownish-grey back had a beige vertebral band. Its back was smooth to slightly granular. Flanks were light with some large warts. The animal had continuous light-colored external folds and distinguishable sacral folds. Its legs exhibited greyish dark crossbars, and its feet lacked metatarsal tubercles. The venter was yellowish. This species lived in syntopy with *P. arnei* in rice paddies around villages in the Daloa region (Kouamé et al., unpub. data).

***Ptychadena pumilio* (Boulenger, 1920)**

Western Dwarf Grass Frog

Material: Female, NGK-Nimba 0069 (Fig. 13H). **Comments:** A female *P. pumilio* was recorded in an open area with a shallow but densely vegetated pond near the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). The species is known from a wide range of habitats from humid to dry savannahs, to open areas in degraded forests, and ranges from southern Mauritania through the savannah belt to eastern Africa (Rödel 2000; Onadeko and Rödel 2008; Padial et al. 2008; Adeba et al. 2010; Channing and Rödel 2019).

***Ptychadena retropunctata* (Angel, 1949)**

Nimba Grass Frog

Material: Two males, NGK-Nimba 0060, NGK-Nimba 0061, and two females, NGK-Nimba 0062, NGK-Nimba

0063 (Fig. 14A). **Comments:** Five *P. retropunctata* were recorded on a high plateau with predominantly grassy mountain pastures and herbaceous vegetation (07°35.453'N, 008°24.957'W; 843 m asl). The SULs of males varied from 28.0–30.5 mm (N = 3), while two females measured 29.0 and 37.5 mm. Whereas four frogs were rust-colored, a female had a deep brown dorsum. In contrast to Rödel (2000) and Channing and Rödel (2019), who describe a white venter, our specimens had a yellow venter. The species was described previously from Mounts Nimba (Angel 1949). Further records became known only from a few montane localities in southeastern Guinea (summarized in Rödel et al. 2004), the Loma Mountains in Sierra Leone (Lamotte 1971), northern Guinea (Hillers et al. 2006), and southeastern Senegal (Monasterio et al. 2016). This is the first country record for *P. retropunctata* in Ivory Coast.

***Ptychadena stenocephala* (Boulenger, 1901)**

Narrow-headed Grass Frog

Material: Two females, NGK-Nimba 0030, NGK-Nimba 0100 (Fig. 14B). **Comments:** Two females of the *Ptychadena stenocephala*-complex (Rödel and Channing 2019) have been found at the edge of a roadside puddle near a heavily degraded forest in the Yéalé village (07°31.928'N, 008°25.401'W; 425 m asl). While they superficially resemble *P. mascareniensis*, e.g., by the ridges and a similar vertebral band (see e.g., Rödel and Glos 2019), they differ from the latter species by reduced webbing, and much more slender body shape (Channing and Rödel 2019). The exact taxonomic status of these frogs requires further research.

***Ptychadena submascareniensis* (Guibé and Lamotte, 1953)**

Small Grass Frog

Material: Three females, NGK-Nimba 0044, NGK-Nimba 0046, NGK-Nimba 0047 (Fig. 14C), and two males, NGK-Nimba 0048, NGK-Nimba 0049 (Fig. 14D). **Comments:** We found a large population of *P. submascareniensis* in predominantly grassy mountain pastures with herbaceous vegetation (07°35.453'N, 008°24.957'W; 843 m asl). There, the species occurred in vast numbers (> 1,500 individuals in an area of approximately 50 ha) during the rainy season. Calling males were observed during the day with peaks between 0830–1030 h GMT and 1830–2000 h GMT. The weather conditions during these observations were characterized by low visibilities due to mist and windy weather. We recorded two migrating individuals in montane grassland in sympatry with *A. cruscum* and *N. occidentalis* (07°35.555'N, 008°25.788'W; 1,235 m asl). These rarely documented frogs (compare Guibé and Lamotte 1953, 1958a; Rödel and Bangoura 2004) have a compact body with a moderately pointed snout. Adult females measured 29.5–32.0 mm (N = 8), while males ranged from 24.0–

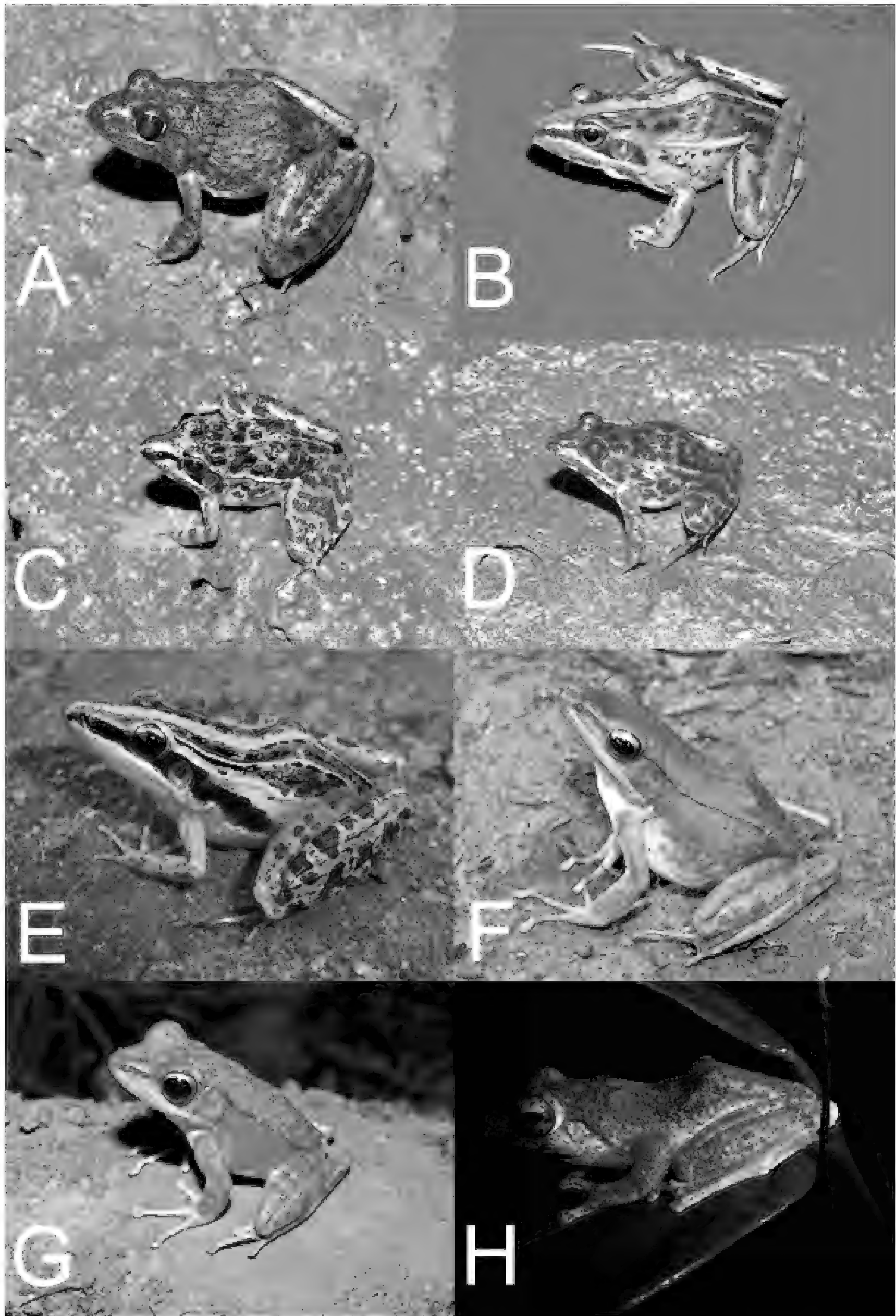


Fig. 14. Ptychadenid, ranid, and rhacophorid frogs from Mount Nimba Integrated Nature Reserve: *Ptychadena retropunctata* (A); *P. stenocephala* female (B); *P. submascareniensis* female (C); *P. submascareniensis* male (D); *P. tournieri* female (E); *Amnirana* sp. 'albolabris west' female (F); *Amnirana* sp. 'albolabris west' male (G); *Chiromantis rufescens* male (H).

27.5 mm (N = 18). According to Channing and Rödel (2019), Mount Nimba is the only known Ivorian site to host *P. submascareniensis*.

***Ptychadena tournieri* (Guibé and Lamotte, 1955)**

Tournier's Grass Frog

Material: Two females, NGK-Nimba 0054, NGK-Nimba 0055 (Fig. 14E), and one male, NGK-Nimba 0056. **Comments:** *Ptychadena tournieri* is widespread in patches of humid and dry savannahs from Senegal into Benin (Rödel 2000; Nago et al. 2006; Adeba et al. 2010; Channing and Rödel 2019). We found the species in open areas, most often among grasses at the edge of plantations. One male measured 35.0 mm, while three females ranged from 39.0–49.0 mm.

Ranidae

***Amnirana* sp. 'albolabris-West'**

West African White-lipped Frog

Material: Female, NGK-Nimba 0101 (Fig. 14F). **Comments:** *Amnirana* sp. 'albolabris-West' is a forest-dwelling frog occurring in the Upper Guinean zone, formerly regarded as being conspecific with the real *A. albolabris* from Central African forests (Jongsma et al. 2018). While its description is being prepared, the occurrence of this species has been even more recently confirmed for Burkina Faso (Ayoro et al. 2020). This taxon was recorded in the Yéalé village, where a chorus was heard at night in a densely vegetated swampy area. One to two males initiated calling and many other males then joined the chorus. A similar behavior was also observed in *A. fonensis* (Kouamé et al., unpub. data). In the Yéalé village, frogs belonging to *A.* sp. 'albolabris-West' were also found in large numbers (N > 50) in a cocoa and coffee plantation near a large pond. Females had a less spiny back than males (Fig. 14G).

Rhacophoridae

***Chiromantis rufescens* (Günther, 1869)**

Western Foam-nest Frog

Material: Male, NGK-Nimba 0102 (Fig. 14H). **Comments:** *Chiromantis rufescens* is a complex of treefrog species (Leaché et al. 2019), occurring in rainforest and the transition zone between forest and savannah, from West and Central Africa to the southernmost record in Angola (Lamotte 1967; Schiøtz 1967; Channing and Rödel 2019; Rödel and Glos 2019; Ernst et al. 2020). They are the only West African species depositing foam nests above stagnant waters (Coe 1967, 1974; Schiøtz 1967; Monayong Ako'o 1978; Rödel et al. 2002). During the entire survey in Mounts Nimba, only one specimen was found on a dark night in a plantation from the Yéalé village dominated by cocoa and coffee trees (Fig. 14H). This specimen measured 45.0 mm in SUL.

Discussion

The amphibian fauna of the Nimba Mountains ranks among the best-known amphibian faunas in West Africa. However, our knowledge is almost completely based on records from the Guinean and Liberian parts of this mountain range (e.g., Guibé and Lamotte 1958a,b, 1963; Xavier 1978; Rödel et al. 2009, 2010; Sandberger et al. 2010; Sandberger-Loua et al. 2018a; Schäfer et al. 2019). Here, we present for the first time a comprehensive summary of the amphibian fauna of the Ivorian part of the mountains.

Such a summary is particularly pressing as the Nimba Mountains, with about 65 amphibian species recorded so far, comprise the most species-rich amphibian site in West Africa (summarized in Rödel et al. 2004; Barej et al. 2015; Schäfer et al. 2019; Channing and Rödel 2019; and several unpublished records), but it is also highly threatened by several factors. The Liberian part had been mined already in the last century (Lamotte 1983), the Guinean part has been prospected for mining and mining will be implemented there soon (J. Doumbia, pers. comm.). In the Ivorian part, natural forest and savannah habitats in the lowlands are imperiled by agricultural encroachment (Woods 2003), and mid-elevation and mountain grasslands are prone to the uncontrolled spread of bush-fires (Lamotte 1959; Hillers et al. 2008b; Sandberger-Loua et al. 2016; this study). Thus, it is important to understand the distributions of species, in particular the endemic and threatened species, of the amphibian fauna.

During our survey we detected 53 amphibian taxa. The smooth skinned, mid-sized squeaker frogs of the *Arthroleptis poecilnotus*-complex likely comprise several species (Rödel and Bangoura 2004), potentially including *A. nimbaensis*. Species which are important finds in this study are *Nimbaphrynoides occidentalis*, *Arthroleptis cruscum*, *Hyperolius nimbae*, *H. soror*, *H. sp.*, and *Kassina cochranæ*, as well as several *Ptychadena* spp. (*arnei*, *pujoli*, *retropunctata*, and *submascareniensis*). These species all have limited ranges in the western part of the Upper Guinea biodiversity hotspot, where at least two of them, *Nimbaphrynoides occidentalis* and *Hyperolius nimbae*, are endemic to the Nimba Mountains (Channing and Rödel 2019)—the first to the montane grasslands and the second to the Ivorian foothills of the mountain. The montane and mid-elevation savannah grasslands of the MNINR are the only known and remaining Ivorian habitats for *N. occidentalis*, *P. retropunctata*, and *P. submascareniensis*. Sandberger-Loua et al. (2016) have shown that *N. occidentalis* comprises three isolated populations, two in Guinea and one in Liberia, however, there is some gene flow (Sandberger-Loua et al. 2018b). So far, it is unclear if the Ivorian records comprise a fourth population or (more likely) are sub-populations of the Guinean populations. Their habitats, the montane grasslands, are

facing the uncontrolled spread of bush-fires. In lowland habitats, human encroachments, forest fragmentation, and steadily increasing agricultural activities, and thus most likely a variety of agrochemicals, are crucial threats for other amphibian species such as *H. nimbae*. However, large areas of dense, broadleaf and evergreen forests, stretching from the lower to mid-elevation slopes, still prevail in MNINR (Fig. 4). Fourteen species, which became known from the Guinean and Liberian parts of the Nimba mountains, could not be detected in this study: *Arthroleptis krokosua*, *A. langeri*, *Sclerophrys chevalieri*, *Africalus weidholzi*, *Hyperolius zonatus*, *Phlyctimantis boulengeri*, *Phrynobatrachus calcaratus*, *P. hieroglyphicus*, *P. maculiventris*, *Ptychadena superciliaris*, *P. aff. aequiplicata*, *Odontobatrachus natator*, *Amnirana occidentalis*, *Geotrypetes pseudoangeli*, and *G. seraphini*. One further species, *Kassina lamottei*, was reported previously from the Ivorian Nimba area, but likewise could not be recorded here. The latter species seems to require large pristine lowland rainforests and reproduces in larger, stagnant ponds (but not in rivers or puddles). In Taï National Park, it was one of the most sensitive species concerning forest alteration (Rödel and Ernst 2001a; Ernst and Rödel 2005; Ernst et al. 2006).

For most of these species, our searching methods, which included acoustic sampling, should be efficient, as shown by our estimation curves indicating sufficient sampling effort for the species richness that occurs in the Ivorian sector of Mounts Nimba. Additionally, many species are more readily detected by their calls than sight, and as frogs were not active at all times, most of them are naturally rare and hide well, and thus are difficult to detect. Some may have escaped our attention in the field, e.g., tree-frogs hiding in the canopy. In order to find caecilians, which mainly live underground, we would have needed to dig in the most promising habitats. However, it is absolutely possible that at least some of these species are absent from the Ivorian slopes of the mountain. For instance, *Arthroleptis langeri* is only known from a few individuals of the Guinean part of Mount Nimba and isolated populations in Liberia (Nopper et al. 2012), while *Phrynobatrachus maculiventris* has been confirmed from a few sites in Guinea and Liberia (Rödel et al. 2009), and *P. hieroglyphicus* is only known from the type specimen and a locality in Liberia (Rödel et al. 2010). However, some other species, like *Phlyctimantis boulengeri*, are known to occur even in disturbed habitats (Rödel and Ernst 2001b, 2003), and thus were expected to occur in MNINR as well. Likewise, our search for *Kassina lamottei* in Zéalé, a formerly known Ivorian lowland locality from the eastern flanks of Mounts Nimba (Schiotz 1967), remained unsuccessful (NG Kouamé et al., unpub. data). There, primary forest has been cleared completely and new asphalted concrete roads facilitate commerce between Ivory Coast and Guinea (NG Kouamé, pers. obs.).

With 53 amphibian taxa, the MNINR is less diverse compared to the known species records in the Guinean part of the Nimba Mountains (Guibé and Lamotte 1958a,b, 1963; Xavier 1978; Rödel et al. 2009, 2010; Sandberger et al. 2010; Sandberger-Loua et al. 2018a; Schäfer et al. 2019). However, the Guinean part has a much larger area (12,540 ha) with a broader range of forested habitats, thus representing the most significant part of the Nimba mountain chain. As part of a set of discontinuous montane reliefs, the Upper Guinea mountain ranges extend along a northwest-southeast line from the Fouta Djallon massif in western Guinea to the regions of Danané and Man in Ivory Coast. The western slopes of these mountains generally receive higher precipitation than the eastern slopes (Rödel and Bangoura 2004; Lauginie 2007; Sandberger-Loua et al. 2017). As a consequence, the Ivorian slopes comprise more savannah patches. This may also explain the restriction of *H. nimbae* to the eastern slopes, as this reedfrog seems to prefer the transition zone between forest and savannah (Kouamé et al. 2016; this study). Nevertheless, when comparing various amphibian assemblages, both Nimba slopes share the highest faunal similarity in the region (comparing Table 3 and Appendix). Compared with other nearby sites, the amphibian species richness of MNINR is also higher than those of Mount Sangbé National Park (Rödel 2003), Diécké Forest Reserve (Rödel et al. 2004), Ziama Forest (Chabanaud 1920, 1921; Böhme 1994a, 1994b), and the Pic de Fon-Simandou range (Parker 1936; Taylor 1968; Rödel and Bangoura 2004). Still, MNINR shares a high number of amphibian species (48–72%) with these sites. Interestingly two range restricted species, e.g., *Conraua cf. allenii* (Fig. 8A–B) and *Odontobatrachus arndti* (Fig. 11B), are known from the Guinean part of Mounts Nimba (Barej et al. 2015; Schäfer et al. 2019), the MNINR (this study), and the adjacent Mount Sangbé National Park (Rödel 2003). This may indicate an area of unique amphibian composition. For instance, the *Conraua* spp. from Mount Sangbé, and potentially those from MNINR, differ in call characteristics from those in more southern Ivorian localities (Rödel and Branch 2002; M.-O. Rödel, unpub. data). The cryptic reedfrog, *Hyperolius* sp. (Fig. 10G–H), needs further investigation because it may represent an undescribed species. Compared with other pristine forest areas, the species richness of MNINR is in the range of Taï National Park in southwestern Ivory Coast (Rödel and Ernst 2004; Ernst et al. 2006; Table 3 and Appendix). Although the Taï National Park is a lowland habitat, it shares 62% of the amphibian species with our study area, emphasising the high diversity of the Upper Guinea rainforests. In addition to this richness of lowland rainforest, the Nimba Mountains are thought to be a refuge area where different faunas met and survived. For instance, *Arthroleptis krokosua* is otherwise only known from Ghana and Guinea, and in contrast *Odontobatrachus arndti* and *O. natator* may be in contact with each other

on the southwestern slopes of the mountain. Some species are endemic to the area (*N. occidentalis*, *H. nimbae*), or seem to have their range center there: *A. cruscum*, *Kassina cochranæ*, *Ptychadena retropunctata*, *P. submascareniensis*, *P. arnei*, and *P. pujoli*. The Nimba Mountains are supposed to have represented a forest refugium during dry Pleistocene times (Maley 1996), thus forest species may have survived unfavorable conditions for prolonged times in this area. Only with strict protection of the Nimba Mountains and its habitats, will such survival be possible in the future as well.

Conclusion

Our discoveries of *Arthroleptis cruscum* and *Ptychadena retropunctata* added two species to the list of the amphibian fauna of Ivory Coast. The unique and diverse mosaic of habitats on Mounts Nimba supports numerous species and their ecosystem services. Our results should be taken as a baseline for future management, monitoring, and conservation activities. Most urgently, management efforts should try to mitigate bush-fires in mountain grasslands, e.g., to protect the viviparous Nimba toad, *N. occidentalis*. Furthermore, we recommend the strict protection of the remaining forest habitats. At lower elevations, it is important to encourage local activities concerning reforestation of previously forested areas and the conservation of (sacred) village forests from which some rare or endemic (e.g., *H. nimbae*, *K. cochranæ*, *P. arnei*, *P. pujoli*), as well as threatened species (e.g., *Leptopelis macrotis*) benefit.

Acknowledgements.—We are very indebted to the “Ministère de l’Environnement et du Développement Durable” of Côte d’Ivoire, and in particular the “Office Ivoirien des Parcs et Réserves, Direction de Zone Ouest” for permitting the research. We would like to acknowledge the local populations of Danané villages for their hospitality, and are especially grateful for the support and collaboration from Paul Seu, elder of Kouan-Houlé. We furthermore thank Nicolas Granier, a conservationist of the Biotopie Foundation France, for facilitating relationships between the local people of Yéalé and our team. We are also thankful to Doh David Gueu, Berthé Zangbéli, and Zoda Alphonse Tokpa, our local assistants and field guides, for their invaluable help during the field work. We would like to acknowledge Alan Channing and Raffael Ernst for their constructive role as reviewers, improving the manuscript. We are grateful to Werner Conradie for the valuable comments he added regarding our manuscript.

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Amphibians of the Nimba Mountains (Ivorian part)



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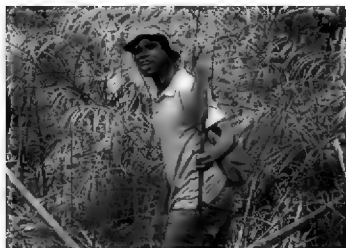
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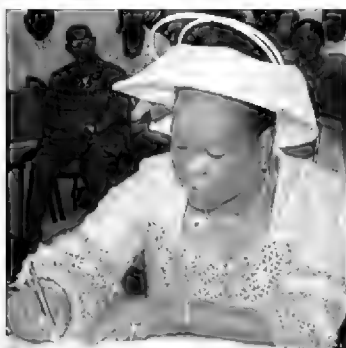
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Germain Gourène is the professor and founder of the “Laboratoire d’Environnement et de Biologie Aquatique” at the Université d’Abobo-Adjamé (actually Université Nangui Abrogoua, Abidjan, Ivory Coast). His research focuses on the systematics and taxonomy of fishes, with an emphasis on Africa; other areas covered include ecology and aquaculture. In addition to his research interest on fishes, Germain is interested in the conservation of aquatic invertebrates and amphibians in the Banco National Park. Germain has served as Vice-President and President of the University of Abobo-Adjamé for 10 years, and was elected as deputy of the locality of Kounahiri (Central Ivory Coast) from 2012–2016.



Mark-Oliver Rödel is the head of the department of “Diversity Dynamics” at the Museum für Naturkunde, Berlin, Germany. He has studied the systematics, taxonomy, biogeography, and ecology of African amphibians for almost 30 years. With his group, comprising students from around the world, he currently runs projects in Germany, Guinea, Ivory Coast, Cameroon, Mozambique, and Malaysian Borneo. His special interest is on how species and ecological communities react to environmental changes. He has authored or co-authored more than 350 scientific publications, including several books.

Appendix. Checklist of the amphibian species recorded in some mountain, highland, and lowland areas of the western part of the Upper Guinean zones. Abbreviations: LF = Lowland Forest; LMEF = Lowland to Mid-Elevation Forest; DCF = Diéké Classified Forest (Rödel et al. 2004); FD = Fouta Djallon Highlands (Hillers et al. 2008a; Barej et al. 2015); MB = Mount Béro (Rödel et al. 2004); MN (Guinea) = Mount Nimba in Guinea (Guibé and Lamotte 1958a, 1963; Laurent 1958; Schiøtz 1967; Lamotte and Ohler 1997, 2000; Rödel et al. 2004; Barej et al. 2015; Sandberger-Loua et al. 2018; Schäfer et al. 2019); MP = Mount Péko National Park (Rödel and Ernst 2003); MS = Mount Sangbé National Park (Rödel 2003; Barej et al. 2015); SR = Simandou range (Parker 1936; Taylor 1968; Rödel and Bangoura 2004); TNP = Taï National Park (Rödel and Ernst 2004; Ernst et al. 2006); ZCF = Ziamia Classified Forest (Böhme 1994a,b; Chabanaud 1920, 1921). Literature records follow recent taxonomic changes.

| Taxa | Western Ivory Coast | | | | Guinea | | | | | |
|--|-----------------------------|----|----|-----|-----------------------------|----|----|----|-----|------|
| | Mountain and highland areas | | | LF | Mountain and highland areas | | | | | LMEF |
| | MN (this study) | MP | MS | TNP | FD | MB | MN | SR | ZCF | DCF |
| Dermophiidae | | | | | | | | | | |
| <i>Geotrypetes pseudoangeli</i> | | | | | | | | X | | |
| <i>Geotrypetes seraphini</i> | | | | X | | | X | X | X | |
| Arthroleptidae | | | | | | | | | | |
| <i>Arthroleptis crusculum</i> | X | | | | | | X | | | |
| <i>Arthroleptis krokosua</i> | | | | | | | X | | | |
| <i>Arthroleptis poecilonotus</i> -complex* | X | X | X | X | X | X | X | X | X | X |
| <i>Astylosternus occidentalis</i> | X | X | X | X | X | | X | X | X | |
| <i>Cardioglossa occidentalis</i> | X | | | X | | X | X | X | | X |
| <i>Leptopelis bufonides</i> | | | | | X | | | | | |
| <i>Leptopelis macrotis</i> | X | | | X | | | X | X | | X |
| <i>Leptopelis occidentalis</i> | X | | X | X | | | | | | |
| <i>Leptopelis spiritusnoctis</i> | X | X | X | X | X | X | X | X | | X |
| <i>Leptopelis viridis</i> | X | X | X | | X | | X | X | X | |
| Bufonidae | | | | | | | | | | |
| <i>Nimbaphrynoides occidentalis</i> | X | | | | | | X | | | |
| <i>Sclerophrys chevalieri</i> | | | | X | | X | X | X | X | X |
| <i>Sclerophrys maculata</i> | X | X | X | X | X | X | X | X | X | X |
| <i>Sclerophrys regularis</i> | X | | X | X | X | | X | X | X | X |
| <i>Sclerophrys taiensis</i> | | | | X | | | | | | |
| <i>Sclerophrys togoensis</i> | X | | | X | | X | X | X | | X |
| Conrauidae | | | | | | | | | | |
| <i>Conraua alleni</i> | X | | X | | | X | X | X | | X |
| <i>Conraua</i> sp. ‘fouta’ | | | | | X | | | | | |
| Dicroglossidae | | | | | | | | | | |
| <i>Hoplobatrachus occipitalis</i> | X | X | X | X | X | | X | X | X | X |
| Hemisotidae | | | | | | | | | | |
| <i>Hemisus guineensis</i> | | X | | X | | | | | | |
| <i>Hemisus marmoratus</i> | X | | X | | | | X | X | | |
| Hyperoliidae | | | | | | | | | | |
| <i>Acanthixalus sonjae</i> | | | | X | | | | | | |
| <i>Afixalus dorsalis</i> | X | | X | X | | X | X | X | X | X |
| <i>Afixalus fulvovittatus</i> | X | | | | | X | X | X | X | X |
| <i>Afixalus nigeriensis</i> | | | | X | | | | | | |
| <i>Afixalus vibekensis</i> | | | | X | | | | | | |
| <i>Afixalus vittiger</i> | | | X | | | | | X | | |
| <i>Afixalus weidholzi</i> | | | X | | | | X | | X | |

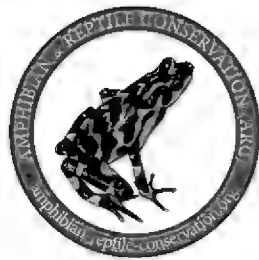
Amphibians of the Nimba Mountains (Ivorian part)

Appendix (continued). Checklist of the amphibian species recorded in some mountain, highland, and lowland areas of the western part of the Upper Guinean zones. Abbreviations: LF = Lowland Forest; LMEF = Lowland to Mid-Elevation Forest; DCF = Diéké Classified Forest (Rödel et al. 2004); FD = Fouta Djallon Highlands (Hillers et al. 2008a; Barej et al. 2015); MB = Mount Béro (Rödel et al. 2004); MN (Guinea) = Mount Nimba in Guinea (Guibé and Lamotte 1958a, 1963; Laurent 1958; Schiøtz 1967; Lamotte and Ohler 1997, 2000; Rödel et al. 2004; Barej et al. 2015; Sandberger-Loua et al. 2018; Schäfer et al. 2019); MP = Mount Péko National Park (Rödel and Ernst 2003); MS = Mount Sangbé National Park (Rödel 2003; Barej et al. 2015); SR = Simandou range (Parker 1936; Taylor 1968; Rödel and Bangoura 2004); TNP = Taï National Park (Rödel and Ernst 2004; Ernst et al. 2006); ZCF = Ziama Classified Forest (Böhme 1994a,b; Chabanaud 1920, 1921). Literature records follow recent taxonomic changes.

| Taxa | Western Ivory Coast | | | | Guinea | | | | | |
|---|-----------------------------|----|----|-----|-----------------------------|----|----|----|-----|------|
| | Mountain and highland areas | | | LF | Mountain and highland areas | | | | | LMEF |
| | MN (this study) | MP | MS | TNP | FD | MB | MN | SR | ZCF | DCF |
| <i>Hyperolius chlorosteus</i> | X | X | X | X | | X | X | X | | X |
| <i>Hyperolius concolor</i> | X | X | X | X | | X | X | X | X | X |
| <i>Hyperolius fusciventris fusciventris</i> | X | X | | X | | X | X | X | X | X |
| <i>Hyperolius guttulatus</i> | X | X | X | X | | | X | | | X |
| <i>Hyperolius igbettensis</i> | | | X | | | | | X | | |
| <i>Hyperolius lamottei</i> | X | X | | | | X | X | X | | |
| <i>Hyperolius nimbae</i> | X | | | | | | | | | |
| <i>Hyperolius nitidulus</i> | | | X | | X | X | X | X | X | |
| <i>Hyperolius occidentalis</i> | | | | | X | | | | | |
| <i>Hyperolius picturatus*</i> | X | X | X | X | X | X | X | X | X | X |
| <i>Hyperolius soror</i> | X | | | X | | | X | | X | |
| <i>Hyperolius</i> cf. <i>sylvaticus</i> | X | | | X | | | | | | |
| <i>Hyperolius zonatus</i> | | | X | X | | X | X | | X | X |
| <i>Hyperolius</i> sp. ‘lamtoensis’ | | | | X | | | | | | |
| <i>Hyperolius</i> sp. ‘Ziama’ | | | | | | | | | X | |
| <i>Hyperolius</i> sp. | X | | | | | | | | | |
| <i>Kassina arboricola</i> | | X | X | | | | | | | |
| <i>Kassina cochranæ</i> | X | | | | | | X | X | X | |
| <i>Kassina fusca</i> | | | X | | X | | | | | |
| <i>Kassina lamottei</i> | | | | X | | | | | | |
| <i>Kassina schioetzi</i> | | X | X | | | | | | | |
| <i>Kassina senegalensis</i> | | | X | | X | | | | | |
| <i>Phlyctimantis boulengeri</i> | | X | | X | | | | | | X |
| Odontobatrachidae | | | | | | | | | | |
| <i>Odontobatrachus arndti</i> | X | | X | | | | X | | | |
| <i>Odontobatrachus fouta</i> | | | | | X | | | | | |
| <i>Odontobatrachus natator</i> | | | | | | X | | X | | |
| <i>Odontobatrachus smithi</i> | | | | | X | | | | | |
| <i>Odontobatrachus ziama</i> | | | | | | | | X | X | |
| Phrynobatrachidae | | | | | | | | | | |
| <i>Phrynobatrachus alleni</i> | X | X | X | X | | X | X | X | X | X |
| <i>Phrynobatrachus annulatus</i> | X | | | X | | | X | X | | |
| <i>Phrynobatrachus calcaratus</i> | | | X | X | X | | X | | | |
| <i>Phrynobatrachus francisci</i> | X | | X | | | | | | | |
| <i>Phrynobatrachus fraterculus</i> | X | | | X | | | X | X | | X |
| <i>Phrynobatrachus guineensis</i> | X | | | X | | | X | X | | X |
| <i>Phrynobatrachus gutturosus*</i> | X | X | X | X | | | X | X | | X |

Appendix (continued). Checklist of the amphibian species recorded in some mountain, highland, and lowland areas of the western part of the Upper Guinean zones. Abbreviations: LF = Lowland Forest; LMEF = Lowland to Mid-Elevation Forest; DCF = Diéké Classified Forest (Rödel et al. 2004); FD = Fouta Djallon Highlands (Hillers et al. 2008a; Barej et al. 2015); MB = Mount Béro (Rödel et al. 2004); MN (Guinea) = Mount Nimba in Guinea (Guibé and Lamotte 1958a, 1963; Laurent 1958; Schiøtz 1967; Lamotte and Ohler 1997, 2000; Rödel et al. 2004; Barej et al. 2015; Sandberger-Loua et al. 2018; Schäfer et al. 2019); MP = Mount Péko National Park (Rödel and Ernst 2003); MS = Mount Sangbé National Park (Rödel 2003; Barej et al. 2015); SR = Simandou range (Parker 1936; Taylor 1968; Rödel and Bangoura 2004); TNP = Taï National Park (Rödel and Ernst 2004; Ernst et al. 2006); ZCF = Ziamia Classified Forest (Böhme 1994a,b; Chabanaud 1920, 1921). Literature records follow recent taxonomic changes.

| Taxa | Western Ivory Coast | | | | Guinea | | | | | |
|--|-----------------------------|----|----|-----|-----------------------------|----|----|----|-----|------|
| | Mountain and highland areas | | | LF | Mountain and highland areas | | | | | LMEF |
| | MN (this study) | MP | MS | TNP | FD | MB | MN | SR | ZCF | DCF |
| <i>Phrynobatrachus latifrons</i> | X | X | | X | X | X | X | X | X | X |
| <i>Phrynobatrachus liberiensis</i> | X | X | X | X | | X | X | X | | X |
| <i>Phrynobatrachus natalensis</i> | X | | X | | X | X | X | X | | X |
| <i>Phrynobatrachus phyllophilus</i> | X | X | | X | | | X | X | | X |
| <i>Phrynobatrachus plicatus</i> | | X | X | X | | X | X | X | | X |
| <i>Phrynobatrachus taiensis</i> | | | | X | | | | | | |
| <i>Phrynobatrachus tokba</i> | X | | X | X | X | X | X | | X | X |
| <i>Phrynobatrachus villiersi</i> | | | | X | | | | | | |
| <i>Phrynomantis microps</i> | | | X | | | | | | | |
| Pipidae | | | | | | | | | | |
| <i>Xenopus tropicalis</i> | X | X | X | X | | | X | X | X | X |
| Ptychadenidae | | | | | | | | | | |
| <i>Ptychadena</i> aff. <i>aequiplicata</i> * | | X | X | X | | | X | X | X | X |
| <i>Ptychadena arnei</i> | X | | | | | | | | | |
| <i>Ptychadena bibroni</i> | X | X | X | X | X | | X | X | X | X |
| <i>Ptychadena longirostris</i> | X | X | X | X | X | | X | X | X | X |
| <i>Ptychadena mascareniensis</i> * | | | X | X | | X | X | X | X | X |
| <i>Ptychadena oxyrhynchus</i> | X | | | | X | | X | X | | |
| <i>Ptychadena pujoli</i> | X | | | | | | X | | | |
| <i>Ptychadena pumilio</i> | X | | X | X | X | X | | X | | X |
| <i>Ptychadena retropunctata</i> | X | | | | | X | X | X | | |
| <i>Ptychadena schillukorum</i> | | X | | | | | | | | |
| <i>Ptychadena stenocephala</i> | X | | X | | | | | | | |
| <i>Ptychadena submascareniensis</i> | X | | | | | X | X | X | | |
| <i>Ptychadena superciliaris</i> | | | | X | | | X | X | X | X |
| <i>Ptychadena tellinii</i> | | | X | | X | | | | | |
| <i>Ptychadena tournieri</i> | X | | | | | | X | X | | |
| <i>Ptychadena trinodis</i> | | | | | X | | | | | |
| Pyxicephalidae | | | | | | | | | | |
| <i>Aubria subsigillata</i> | | | | X | | | | | | |
| Ranidae | | | | | | | | | | |
| <i>Amnirana fonensis</i> | | | | | | | | X | | |
| <i>Amnirana galamensis</i> | | | X | | | | | | | |
| <i>Amnirana occidentalis</i> | | | | X | | | X | X | X | X |
| <i>Amnirana</i> sp. ‘albolabris west’ | X | X | X | X | | X | X | X | X | X |
| Rhacophoridae | | | | | | | | | | |
| <i>Chiromantis rufescens</i> | X | X | | X | | | | | | X |
| Total number of species | 53 | 29 | 44 | 53 | 26 | 28 | 56 | 52 | 31 | 39 |



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A new species of the genus *Gekko* Laurenti, 1768 (Squamata: Gekkonidae) from the Nicobar Archipelago, with an overview of congeners from the Andaman and Nicobar Islands

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Abstract.—A comprehensive systematic review of the genus *Gekko* Laurenti, 1768 in the Andaman and Nicobar archipelago was undertaken. The known members *Gekko verreauxi* Tytler, 1865 and *Gekko (Ptychozoon) nicobarensis* (Das and Vijayakumar, 2009) are redescribed based on new material collected during this study. The systematic status of the *Gekko smithii* (s. lat.) population from the southern Nicobar Islands was reassessed and found to represent a distinct species. Based on morphological and morphometric distinction, this allopatric, insular population is described as *Gekko stoliczkai* sp. nov. Notes on ecology, natural history, morphology, and distribution are presented for all these species, with recommendations on their conservation status.

Keywords. Asia, cryptic species, endemic species, giant gecko, Reptilia, Sundaland

Citation: Chandramouli SR, Gokulakrishnan G, Sivaperuman C, Grismer LL. 2021. A new species of the genus *Gekko* Laurenti, 1768 (Squamata: Gekkonidae) from the Nicobar Archipelago, with an overview of congeners from the Andaman and Nicobar Islands. *Amphibian & Reptile Conservation* 15(1) [Taxonomy Section]: 108–125 (e276).

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Accepted: 1 April 2021; **Published:** 30 June 2021

Introduction

The nocturnal, arboreal members of the true gecko genus, *Gekko* Laurenti, 1768, are currently represented by 77 species, which range from eastern India to Papua New Guinea (Uetz et al. 2020). Wood et al. (2019) recently partitioned *Gekko* into seven subgenera, including two previously recognized genera, *Ptychozoon* Kuhl and van Hasselt, 1822 and *Luperosaurus* Gray, 1845. The Andaman and Nicobar Islands, situated to the east of the Indian peninsula and south of the Ayeyarwady Delta region of Myanmar, lie on the western periphery of the geographic range of the genus *Gekko*. Currently, this genus is represented by three species within the Andaman and Nicobar archipelago, namely *Gekko verreauxi* Tytler, 1865 from the Andaman Islands, *Gekko (Ptychozoon) nicobarensis* (Das and Vijayakumar, 2009) from the Nicobar Islands, and a species from the Nicobar Islands currently identified as *Gekko smithii* Gray, 1842 (Uetz et al. 2020). Of these, *Gekko verreauxi*, the earliest species known from the Andaman and Nicobar Islands, was reported from the Andaman Islands as *Gekko gecko* (Linnaeus, 1758) as early as Blyth (1863). *Gekko*

verreauxi was once considered a synonym of *G. stentor*, which again, was a junior synonym of *G. smithii* (fide Boulenger, 1885) before being revived as a valid species by Ota et al. (1991) based on an examination of type material. This was followed by the report of *Ptychozoon homalocephalum* [now *Gekko (Ptychozoon) nicobarensis*] from the Nicobars by Steindachner (1867), which was apparently overlooked by Das and Vijayakumar (2009). The third species from this Archipelago, *Gekko smithii*, was reported by Biswas and Sanyal (1977) from Great Nicobar as *Gekko gecko* (in this study regarded as *Gekko* cf. *smithii*), based on specimens at the Bombay Natural History Society (BNHS) collected by Humayun Abdulali. Subsequently, Biswas (1984) reported additional *Gekko smithii* (sic) records from the South Andaman and Great Nicobar Islands. Veselý (1999) provided additional notes on the morphology and distribution of *Gekko verreauxi*. Das (1999) speculated that the Nicobar population of *G. smithii* was potentially allied to an undescribed member of this group from Sumatra and specifically distinct from the nominate species, *Gekko smithii*. Here, we examine the three species of *Gekko* of the Andaman and Nicobar Islands; provide additional data on the morphology,

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natural history, and distribution of *G. verreauxi* and *G. (P). nicobarensis*; and reassess the taxonomic status of *Gekko* cf. *smithii* populations from the Nicobar archipelago.

Materials and Methods

Specimens of *Gekko* encountered in the field were gently restrained, measured, scored for morphological characters (see below), photographed, and released at the site of capture. Four specimens of *G. verreauxi* were collected from the Andaman Islands, three specimens of *G. (Ptychozoon) nicobarensis* were collected from Car Nicobar, Camorta, and Teressa Islands, and five specimens of the *G. cf. smithii* were collected from Great and Little Nicobar Islands in and around human habitations between 2014 and 2017. These specimens were preserved in 70% ethanol and are deposited in the two collections of the Zoological Survey of India, Andaman and Nicobar Islands Regional Centre, Port Blair, India (ZSI, ANRC) and the Department of Ocean Studies and Marine Biology (DOSMB), Pondicherry University, Brookshabad, Port Blair, India.

The following measurements (in mm) were recorded with vernier calipers: Snout-vent length (SVL), measured from the snout tip to the anterior edge of the cloaca; tail length (TAL), measured from the posterior edge of the cloaca to the tail tip; trunk length (AG), measured between the axilla and groin; head length (HL), measured from the snout tip to the angle of the jaw; head width (HW), measured at the widest point on the head; head depth (HD), measured from the top of the head to the throat, at the level of the eyeball; horizontal eye diameter (ED), eye-nostril distance (EN), measured from the anterior margin of the eye to the posterior margin of the external nares; snout length (ES), measured from the anterior margin of the eye to the tip of the snout; distance from eye to tympanum (ETY), measured from posterior margin of the eye to the anterior edge of the tympanum; tympanum diameter (TYD), measured across the widest point of the tympanic opening; upper arm length (UAL), measured from the axilla to the elbow; lower arm length (LAL), measured from the elbow to the wrist; palm length (PAL), measured from the wrist to the tip of finger III; thigh length (FEL), measured from the point of insertion of the hind limb on the trunk to the knee; tibia length (TBL), measured from the knee to heel; foot length (FOL), measured from heel to the tip of toe IV; and lengths of fingers (F1–F5) and toes (T1–T5) measured from the fork of the digits to the tip excluding the claws. Supralabials and infralabials were counted along the upper and lower lips from rostral and mental to the gape, respectively. Enlarged scales bordering the mental posteriorly were counted as postmentals, and expressed as inner pair + outer pairs. Ventrals were counted along a transverse series across the underside at mid-body between the ventrolateral

folds; internasals were counted between the nasal scales; subdigital lamellae were counted on the ventral surface of digits of the fingers and toes, and dorsal tubercle rows were counted in a transverse series at the mid-body. GPS coordinates of the localities where the individuals were encountered were recorded with a Garmin GPS MAP 78s and mapped with ARC MAP v. 10. Comparative material of the Sundaic *G. smithii* are provided in the Appendix.

The following analyses were carried out to test the hypothesis that the Nicobar population of *Gekko smithii* is morphologically distinct from those of the Sundaic regions. A Student's *t*-test was conducted on meristic and mensural data (see below) with statistically similar variances (i.e., *p* values > 0.05 in a Levene's test) and normal distributions (i.e., *p* values > 0.05 in a Shapiro-Wilk's *W* test) to search for the presence of statistically significant mean differences (*p* < 0.05) among species across the data set. Boxplots were generated for all characters in order to visualize the range, mean, median, and degree of differences between species pairs bearing statistically different mean values. All statistical analyses were performed in R (v3.4.3). The morphospacial clustering of the sampled individuals was visualized using Principal Component Analysis (PCA) from the ADEGENET package in R (Jombart et al. 2010) implemented by the *prcomp()* command. PCA is a dimension-reducing algorithm that decreases the complexity of a data set by finding a subset of input variables that contain the most relevant information (i.e., the greatest variance in the data) while de-emphasizing those characters that do not, thus increasing the overall accuracy of the results by eliminating noise and the potential for overfitting (Agarwal et al. 2007). PCA is an unsupervised analysis that recovers morphospacial relationships among the sampled individuals (i.e., data points). It is important to note that clusters of conspecific individuals were not pre-defined in the analysis but simply color-coded in the scatter plot in order to observe their positions and morphospacial relationships. Meristic data were log-transformed prior to analysis in order to normalize their distributions, so as to ensure that characters with very large and very low values could not over-leverage the results owing to intervariable nonlinearity. To help remove the potential effects of allometry in the mensural characters, only adults were collected (as determined by SVL). Additionally, variation in adult size was normalized using the following equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where X_{adj} = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVL_{mean} = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000; Tables 1 and 2). The metrics of each species were normalized separately to avoid conflating intra- with interspecific variation (Reists 1986). Meristic and mensural data were not concatenated but analyzed separately owing to differences in sample sizes. All data were scaled to their standard deviations

Table 1. Summary statistics and Principal Component Analysis scores for the meristic characters.

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 |
|------------------------------|--------|--------|--------|--------|--------|--------|
| Standard deviation | 1.384 | 1.217 | 0.994 | 0.860 | 0.813 | 0.463 |
| Proportion of variance | 0.319 | 0.247 | 0.165 | 0.123 | 0.110 | 0.036 |
| Cumulative proportion | 0.319 | 0.566 | 0.731 | 0.854 | 0.964 | 1.000 |
| Eigenvalue | 1.916 | 1.480 | 0.988 | 0.740 | 0.661 | 0.214 |
| Internasals | -0.223 | 0.524 | -0.070 | -0.810 | 0.111 | -0.050 |
| Infralabials | -0.578 | -0.388 | -0.077 | -0.013 | 0.225 | -0.678 |
| Supralabials | -0.633 | -0.265 | -0.138 | -0.026 | 0.019 | 0.714 |
| Postmentals | -0.399 | 0.417 | 0.056 | 0.281 | -0.748 | -0.158 |
| 4 th toe lamellae | -0.153 | 0.026 | 0.974 | -0.008 | 0.155 | 0.057 |
| Ventrals | -0.182 | 0.575 | -0.136 | 0.513 | 0.594 | 0.029 |

to insure they were analyzed on the basis of correlation and not covariance. A Discriminant Analysis of Principal Components (DAPC) was performed on both data sets. The DAPC places individuals from each predefined population into separate clusters (i.e., plots of points) bearing the smallest within-group variance that produce linear combinations of centroids having the greatest between-group variance (i.e., linear distance; Jombart et al. 2010). DAPC relies on scaled data calculated from its own PCA as a prior step to ensure that the variables analyzed are not correlated and number fewer than the sample size. Dimension reduction of the DAPC prior to plotting was accomplished by retaining the first set of PCs that accounted for approximately 90% of the variation in the data set (Jombart and Collins 2015) as determined from a scree plot generated as part of the analysis. Retaining too many PCs forces false structure to appear in the data, while retaining too few runs the risk of missing true structure (Cangelosi and Goriely 2007).

Additional museum abbreviations are: NHMUK – The Natural History Museum, London (formerly, BMNH – British Museum of Natural History), FMNH – Field Museum of Natural History, Chicago, Illinois,

USA; USNM – National Museum of Natural History, Washington, DC, USA; THMNH – Thailand Natural History Museum; LSUHC – La Sierra University, Herpetology Collection; ZMA – Universiteit van Amsterdam, Zoologisch Museum, Amsterdam, Netherlands; ZRC: Zoological Reference Collection, Department of Zoology, University of Singapore.

Results

The results of the analyses support our initial hypothesis that the Nicobar and Sundaic populations of *Gekko smithii* are morphologically distinct. The PCA of the meristic data show that the Nicobar population overlaps with the Sundaic *Gekko smithii* along principal component (PC) 1 but is generally well-separated from Sundaic *G. smithii* along PC 2 (Fig. 1). PC1 accounts for 31.9% of the variation in the data set and loads most heavily for infralabials and supralabials (Table 1), while PC2 accounts for 24.7% of the variation and loads most heavily for postmentals and internasals. Four PC eigenvalues and the first discriminate function were retained for the DAPC, which accounted for 92.9% of the

Table 2. Summary statistics and Principal Component Analysis scores for the mensural characters. Abbreviations are defined in the text.

| | PC1 | PC2 | PC3 | PC4 | PC5 | PC6 | PC7 | PC8 | PC9 | PC10 |
|------------------------|-------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| Standard deviation | 2.713 | 0.930 | 0.745 | 0.589 | 0.526 | 0.442 | 0.364 | 0.348 | 0.318 | 0.221 |
| Proportion of variance | 0.736 | 0.087 | 0.056 | 0.035 | 0.028 | 0.020 | 0.013 | 0.012 | 0.010 | 0.005 |
| Cumulative proportion | 0.736 | 0.822 | 0.878 | 0.912 | 0.940 | 0.960 | 0.973 | 0.985 | 0.995 | 1.000 |
| Eigenvalue | 7.358 | 0.865 | 0.555 | 0.347 | 0.276 | 0.195 | 0.132 | 0.121 | 0.101 | 0.049 |
| HD | 0.322 | -0.250 | -0.109 | 0.009 | 0.738 | -0.011 | -0.071 | 0.165 | -0.426 | -0.251 |
| HL | 0.340 | 0.157 | -0.035 | -0.162 | -0.329 | 0.034 | -0.776 | -0.117 | -0.144 | -0.292 |
| HW | 0.324 | -0.220 | -0.385 | -0.359 | 0.092 | 0.136 | 0.107 | -0.046 | 0.701 | -0.195 |
| TYD | 0.316 | -0.297 | -0.033 | 0.459 | -0.173 | -0.741 | -0.002 | -0.010 | 0.144 | 0.002 |
| EN | 0.320 | -0.270 | -0.117 | 0.381 | -0.404 | 0.529 | 0.336 | -0.091 | -0.260 | -0.182 |
| ES | 0.356 | -0.103 | -0.055 | 0.023 | 0.023 | 0.208 | -0.226 | 0.259 | 0.025 | 0.835 |
| ED | 0.208 | 0.777 | -0.447 | 0.336 | 0.146 | -0.021 | 0.127 | -0.022 | 0.041 | 0.010 |
| UAL | 0.285 | 0.179 | 0.743 | 0.281 | 0.229 | 0.210 | -0.034 | -0.052 | 0.374 | -0.122 |
| LAL | 0.340 | 0.088 | 0.147 | -0.372 | 0.033 | -0.171 | 0.280 | -0.707 | -0.236 | 0.230 |
| AG | 0.327 | 0.222 | 0.215 | -0.398 | -0.265 | -0.181 | 0.348 | 0.615 | -0.144 | -0.127 |

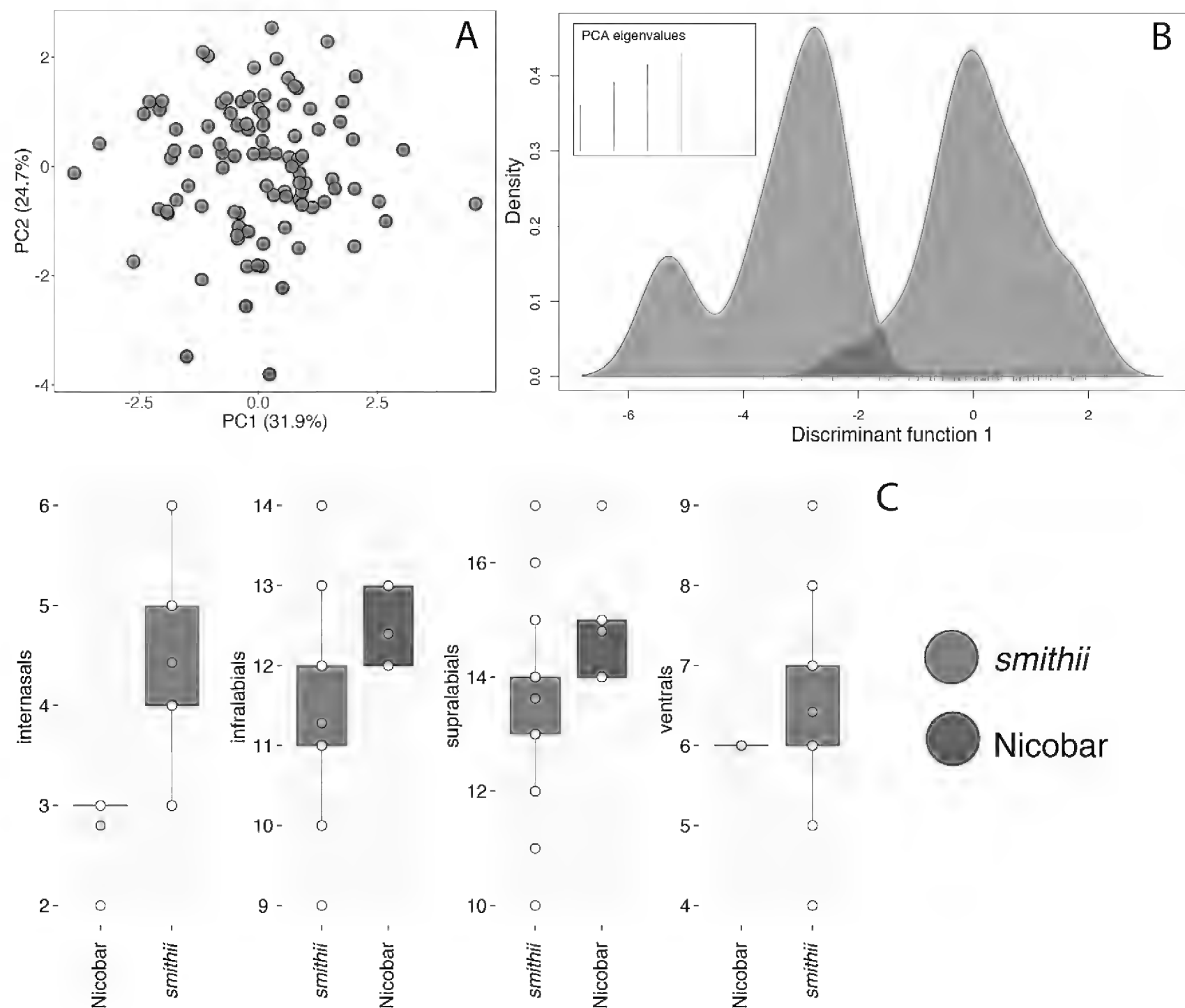


Fig. 1. Analyses of meristic characters. **(A)** First two principal components of the PCA. **(B)** Density curves of the first discriminant function of the DAPC. **(C)** Boxplots in which light-blue circles are the means and the black horizontal bars are the medians.

variation and demonstrated very little overlap between the Nicobar population and *G. smithii*. These results are mirrored by the mensural data, where the PCA of the mensural data show that the Nicobar population and *Gekko smithii* plot completely separately from each other (Fig. 2). PC1 accounts for 73.6% of the variation in the data set and loads fairly evenly for all characters, except for low loadings for the eye diameter and forelimb length (Table 2). PC2 accounts for 8.8% of the variation and loads most heavily for eye diameter. Six PC eigenvalues and the first discriminate function were retained for the DAPC, which accounted for 97.1% of the variation and demonstrated no overlap between the Nicobar population and *G. smithii*. Student *t*-tests also showed several statistically significant mean differences between the Nicobar population and *Gekko smithii* in both meristic and mensural characters (Table 3; Figs. 1–2).

Based on the data presented above, we believe there is sufficient evidence to formulate a robust, testable hypothesis indicating the Nicobar population is a distinct species, and as such, is described below. In addition, we redescribe the species *G. verreauxi* and *G. nicobarensis* based on our new data.

Taxonomy

***Gekko (Gekko) verreauxi* Tytler, 1865 (Figs. 3–4)**
Gekko verreauxi Tytler, 1865
Gekko stentor – Boulenger (1885) part
Gekko smithii – Smith (1935) part

Table 3. Results of Student *t*-tests.

| | <i>p</i> -value | <i>t</i> -value |
|----------------------------|-----------------|-----------------|
| Mensural characters | | |
| Head length | 1.71E-06 | -5.1 |
| Head width | 0.02105 | -2.3457 |
| Snout length | 0.02042 | -2.3577 |
| Eye diameter | 1.65E-10 | -7.1575 |
| Forelimb length | 0.01159 | -2.5737 |
| Tibia length | 2.13E-05 | -4.4714 |
| Axilla-groin length | 8.11E-07 | -5.2777 |
| Meristic characters | | |
| Internasals | 8.40E-07 | -5.2692 |
| Infralabials | 2.23E-02 | 2.3234 |
| Supralabials | 0.028 | 2.2311 |
| Ventrals | 0.003089 | -3.0357 |

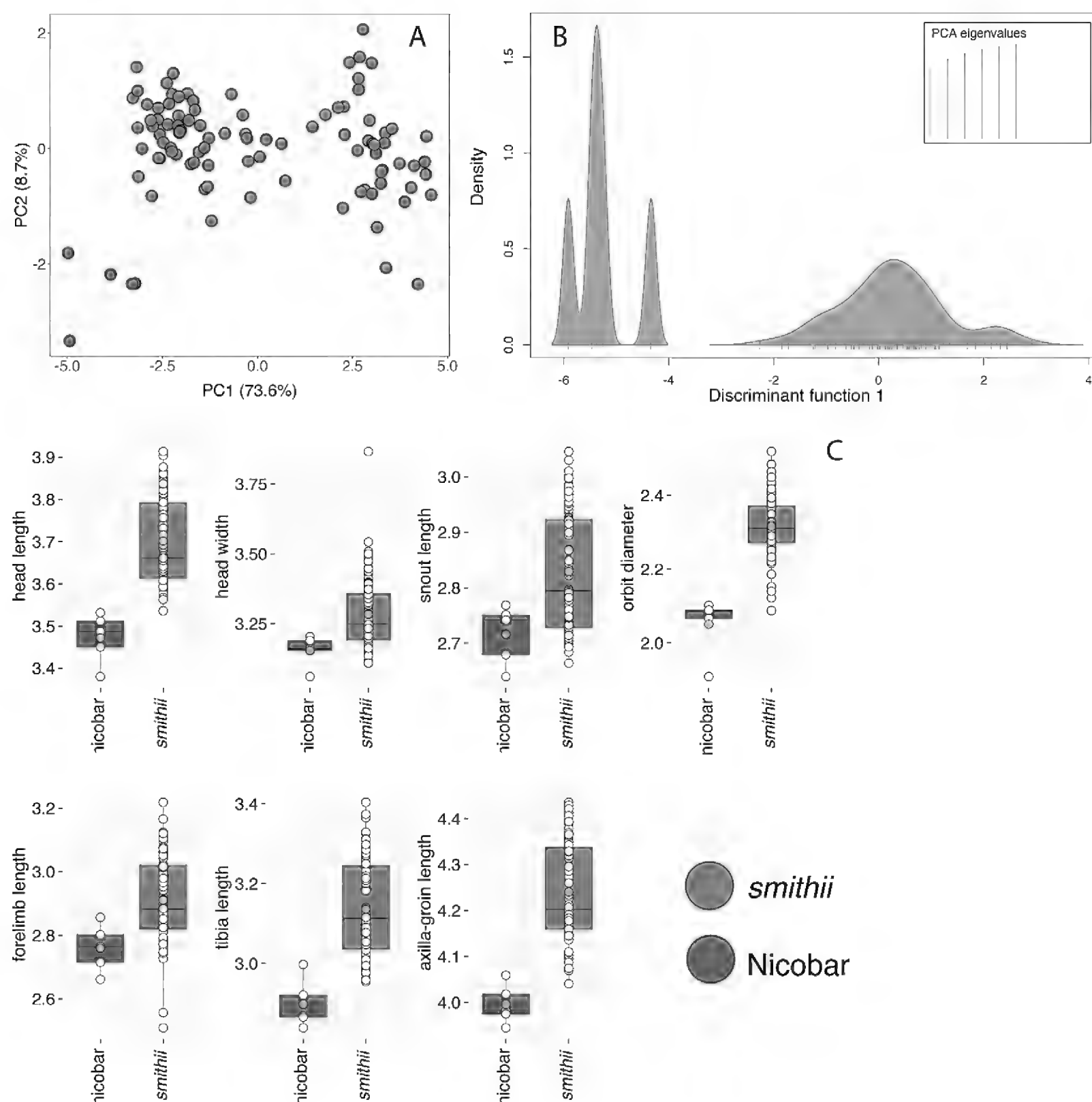


Fig. 2. Analyses of mensural characters. **(A)** First two principal components of the PCA. **(B)** Density curves of the first discriminant function of the DAPC. **(C)** Boxplots in which light-blue circles are the means and the black horizontal bars are the medians.

Lectotype. NHMUK 68.4.3.64, an adult female collected from the ‘Andaman Islands’ by W. Theobald *fide* Ota et al. (1991) (photographs studied).

Paralectotype. NHMUK 1868.4.3.65, an adult female from the same location (photographs studied).

Material studied. ZSI/ANRC/T/4324 from Majarpahar (11.7029°N, 92.6433°E, 16 m asl), South Andaman; ZSI/ANRC/T/3726 from Durgapur (13.2761°N, 93.0311°E, 5 m asl), North Andaman; ZSI/ANRC/T/4566 from Rabindranagar (10.7080°N, 92.5334°E, 57 m asl), Little Andaman; ZSI/ANRC/T/5779 from Krishna Nagar (12.0086°N, 92.9635°E, 58 m asl), Swarajdweep (formerly Havelock Island).

Diagnosis. A large-bodied species of *Gekko* (SVL 140.06–146.48 mm) characterized by: 12–14 supralabials; 9–13 infralabials; two elongate inner pairs of postmentals in

broad contact with each other; two smaller, separated outer pairs of postmentals; 11–13 precloacal pores in males; absence of femoral pores; two internasals in contact with each other; distinct ventrolateral dermal folds; 26–29 transverse rows of imbricate ventrals; 12 or 13 transverse rows of enlarged, rounded, dorsal tubercles; two to three enlarged post-cloacal spurs on each side of the vent; 18–20 undivided subdigital lamellae on toe IV; presence of five legible, dark, transverse bands in juveniles and subadults transforming into a nearly uniform dark-brown dorsal coloration in adults with a pale-white to light-brown venter.

Description and variation. A large species of *Gekko*, measuring 109.55–146.49 mm SVL. Head large (mean HL:SVL 0.26), longer than broad (mean HL:HW 1.19) with a blunt, rounded snout tip. Eyes moderately large (mean ED:HL 0.25) with a vertically elliptical pupil approximately one-half the length of the snout (mean ED:ES 0.53); nostrils situated closer to the snout tip

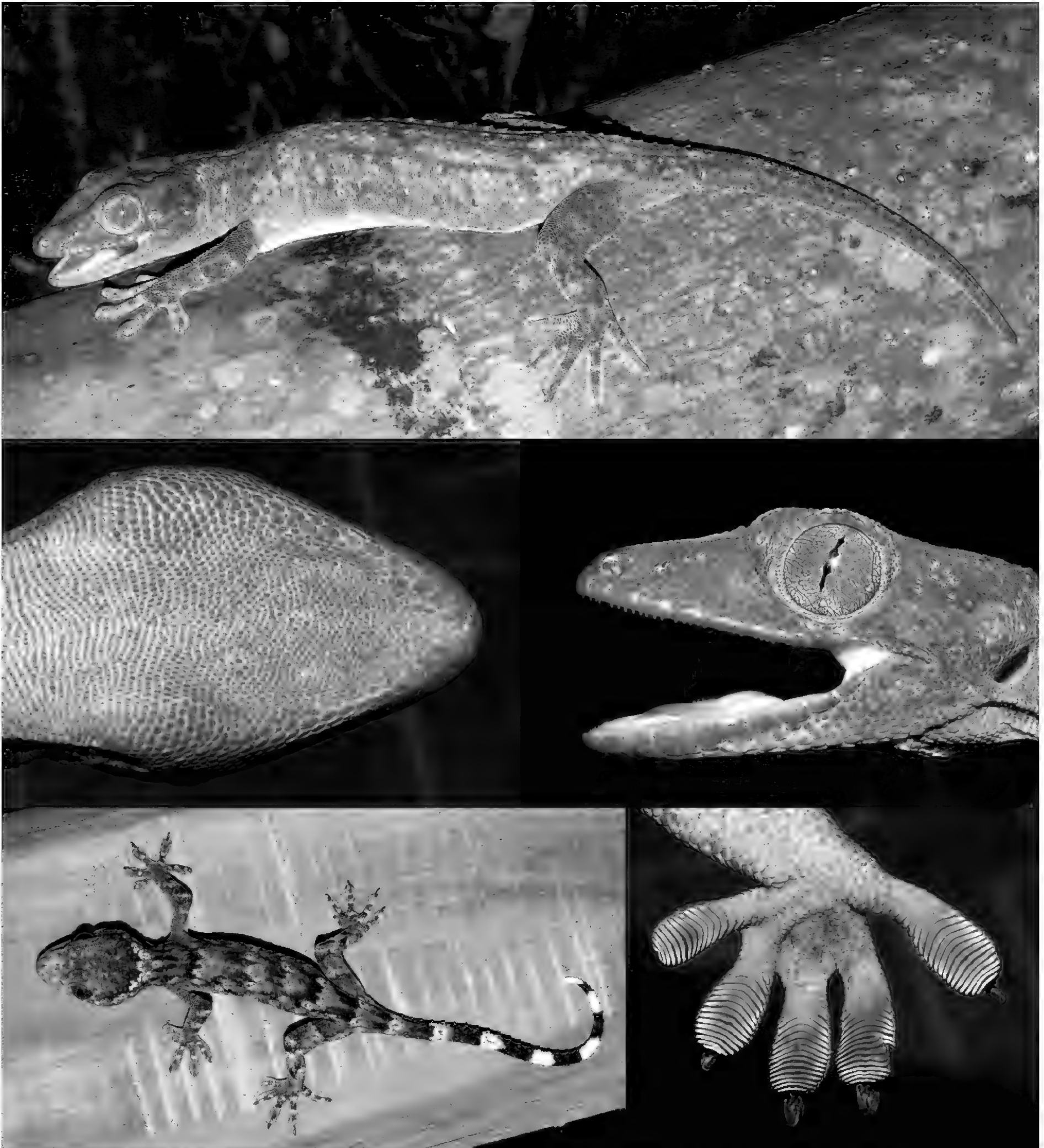


Fig. 3. *Gekko verreauxi* in life from South Andaman (top, middle, and bottom right: adult; bottom left: juvenile).

than to the eyes (mean EN:ES 0.79). Trunk one-half as long as the body (mean AG:SVL 0.46). Overall habitus depressed. Supralabials 12–14 on each side; infralabials 9–13 on each side; two moderately enlarged postmentals in broad medial contact, followed by three smaller pairs of scales. Dorsum bearing 11–13 transverse rows of enlarged tubercles. Ventrals imbricate, in 27–29 transverse rows at midbody. A pair of enlarged, rounded cloacal spurs at the base of the vent. Anterior subcaudals not enlarged, posterior ones slightly enlarged. Upper arm shorter than lower arm (mean UAL:LAL 0.79); palm enlarged with five fingers; the first one with an indistinct

claw; relative lengths of fingers IV>III>V>II>I. Thighs short (mean FEL:SVL 0.16), robust bearing a few tuberculated scales on the dorsal surface. Tibia as long as the thighs (mean TBL:SVL 0.16); toes with entire, undivided subdigital lamellae, 18–20 on toe IV; relative lengths of toes IV>III>V>II>I. Fingers and toes free, lacking membranous skin flaps. Males have a series of 11–13 precloacal pores and lack femoral pores.

Coloration in life. Overall dorsal coloration uniform dark- to light-brown with five to six darker transverse bands on the body and five or six on the tail. Venter

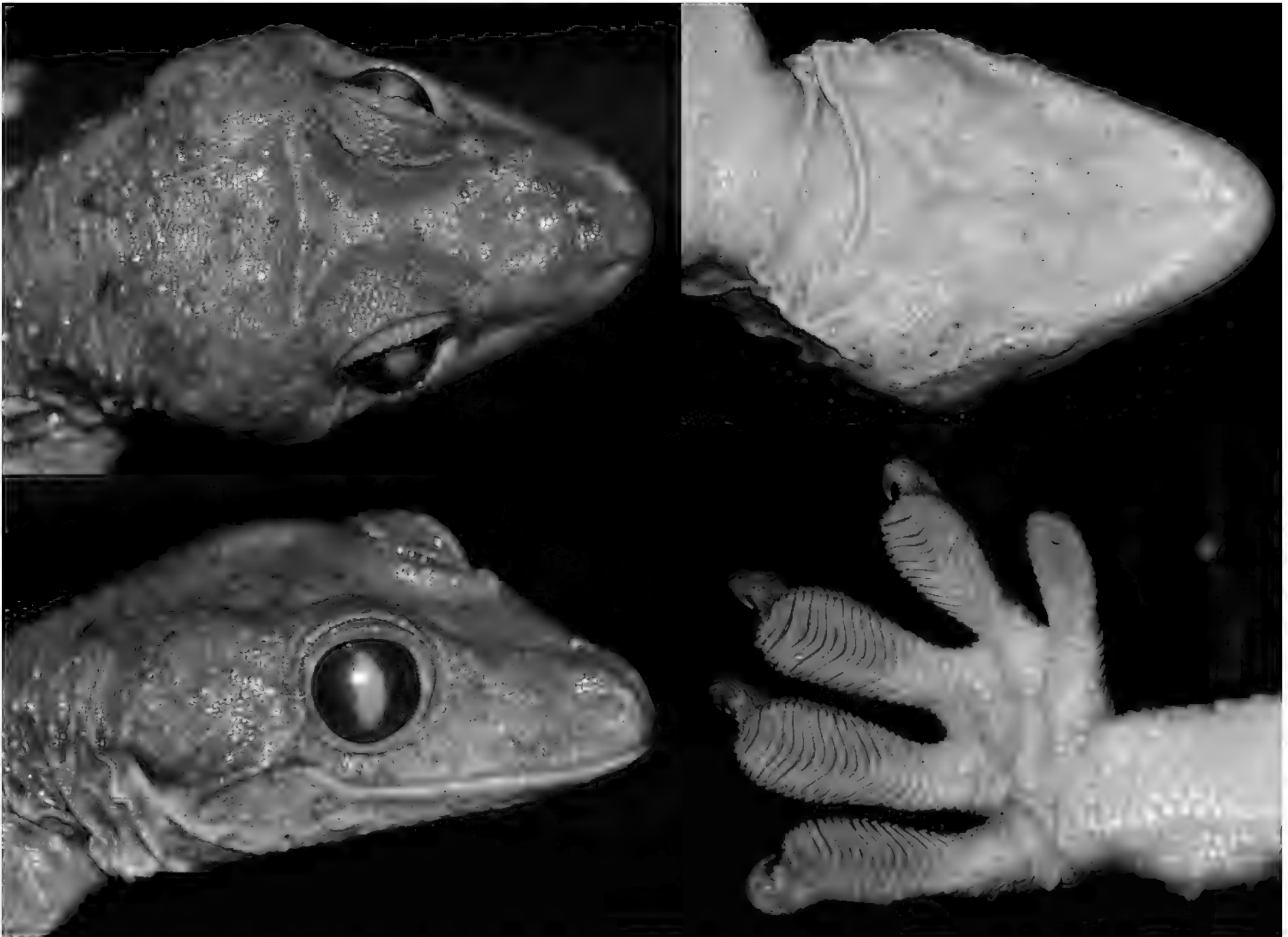


Fig. 4. Dorsal, ventral, and lateral views of the head and ventral view of the foot of *Gekko verreauxi* (ZSI ANRC T 4566).

uniform brown and lacking any specific pattern. Eyes with vertically elliptical pupils and a greenish yellow iris.

Distribution. Occurs throughout the Andaman Islands, and was recorded from the following islands during the present study: South, Middle, North and Little Andaman, Rutland Island, Ritchie's archipelago (Havelock, Neil, John Lawrance, and Henry Lawrance), Kyd, Labyrinth archipelago (Tarmugli, Alexandra, Hobday, and Redskin), Interview, North Reef, Paget, Long, Guitar, and North Passage Islands (Fig. 10).

Natural history. Nocturnal in habit. Found on tall trees at a height of approximately 5 m and above the ground in evergreen forests. It has also been recorded from secondary forests, human habitations, and littoral forests. Calls comprise of a series of repeatedly uttered, rattling syllables of *tuk-tuk-tuk-tuk*.

Remarks. Boulenger (1885) synonymized *Gekko verreauxi* under *Gekko stentor* (Cantor, 1847), a junior synonym of *Gekko smithii* Gray, 1842. Ota et al. (1991), while revalidating *G. verreauxi* from the synonymy of *G. smithii*, provided a detailed redescription of the species with measurements and scale-counts from both the lectotype and the paralectotype. Both of these specimens are females and hence, we have supplemented

the available information with new specimens, including males, in order to improve our understanding of the species. The lectotype has 14 supralabials (12–14 in our material), 10 infralabials (9–13), 11 rows of dorsal tubercles at midbody (11–13), and 21 subdigital lamellae (18–20) under toe IV.

***Gekko (Ptychozoon) nicobarensis* (Das and Vijayakumar, 2009) (Figs. 5–6)**

Ptychozoon homalocephalum – Steindachner (1867)

Ptychozoon kuhli – Stoliczka (1870); Smith (1935); Biswas and Sanyal (1977); Das (1999) part

Holotype. ZSI 2603, an adult male collected by A.R. Anderson from 'Nicobars' in the late 1800s.

Material studied. DOSMB05102 from Chuckchuka (9.2161°N, 92.8109°E, 14 m asl), Car Nicobar, ZSI/ANRC/T/5234 from Kalasi (8.2803°N, 93.1173°E), Teresa, and ZSI/ANRC/T/4235 from Chota Enaka (8.0657°N, 93.5428°E, 39 m asl), Camorta, Nicobar Islands.

Diagnosis. A medium to large-bodied (SVL 78.2–95.8 mm) species of *Gekko*, characterized by: presence of extensive, membranous skin flaps along the sides of the head, trunk, and tail; tail tip with an oval shaped

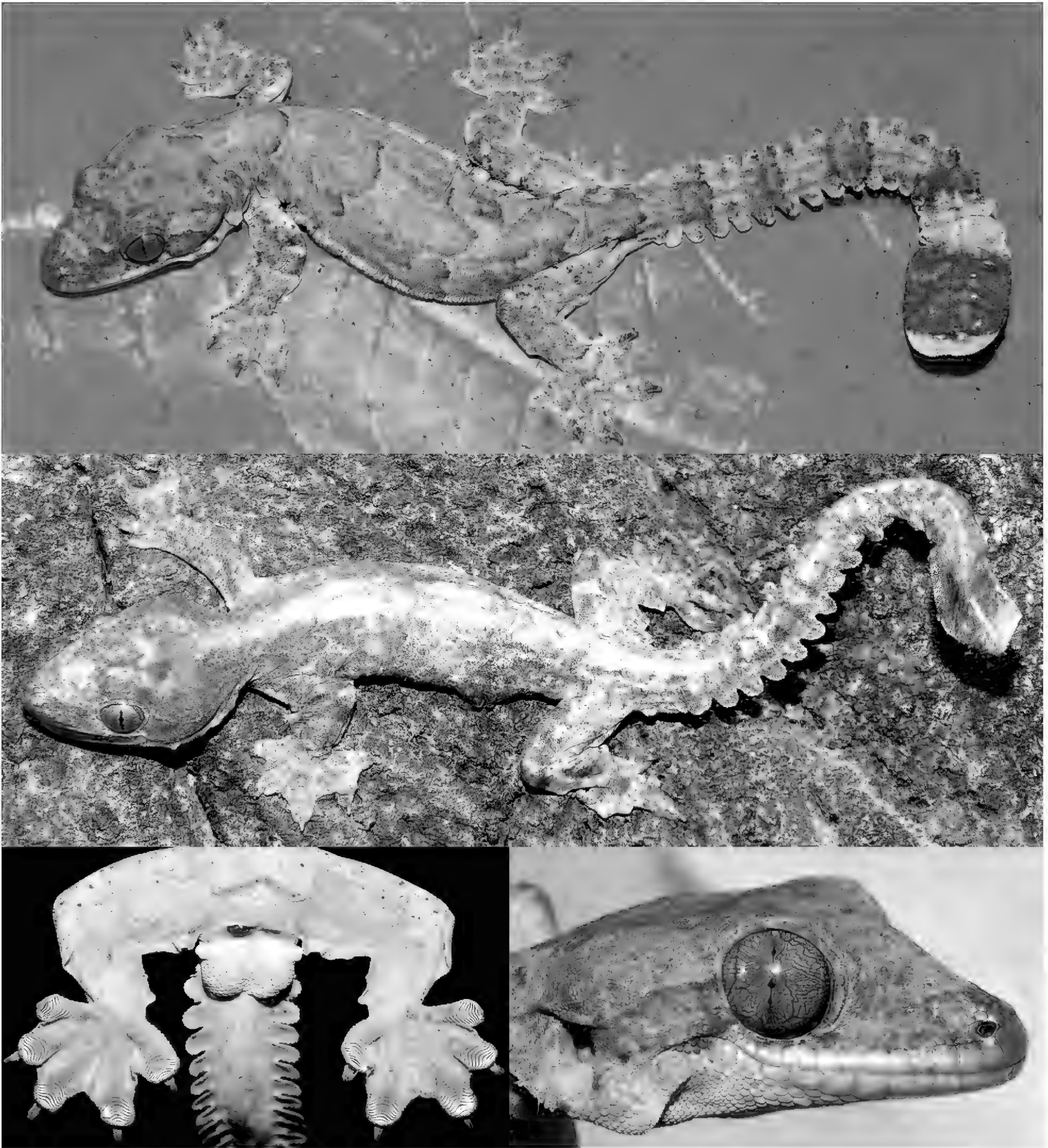


Fig. 5. *Gekko (Ptychozoon) nicobarensis* in life from Car Nicobar (above: banded; middle: striped morphs).

skin flap; presence of 10–13 supralabials; 10 or 11 infralabials; two relatively small, elongate inner pairs of postmentals in broad medial contact with each other; three smaller, separated outer pairs of postmentals; 20–21 precloacal pores in males, no femoral pores; two internasals in contact with or separated by one or two small azygous scales; no ventrolateral body folds; 29–32 transverse, juxtaposed rows of ventrals; four well-spaced, transverse rows of enlarged, rounded dorsal tubercles; one enlarged post-cloacal spur on each side of the vent; 13–21 undivided subdigital lamellae on toe IV; dorsal color pattern consisting of four or five legible, dark, W-shaped, transverse bands or a light-colored vertebral

stripe bounded on either side by two darker stripes, and a creamy white to light-brown venter.

Description and variation. A medium to large-bodied species of *Gekko* belonging to the subgenus *Ptychozoon* measuring 78.42–95.86 mm SVL, head large (mean HL:SVL 0.28), much longer than broad (mean HL:HW 1.34) with a blunt, rounded snout tip. Eyes protruding, fairly large (mean ED:HL 0.25) with a vertically elliptical pupil; eye nearly half as long as the snout (mean ED:ES 0.53); nostrils situated closer to the snout tip than to the eyes (mean EN:ES 0.77). Trunk much shorter than one-half the length of the body (mean AG:SVL 0.47).

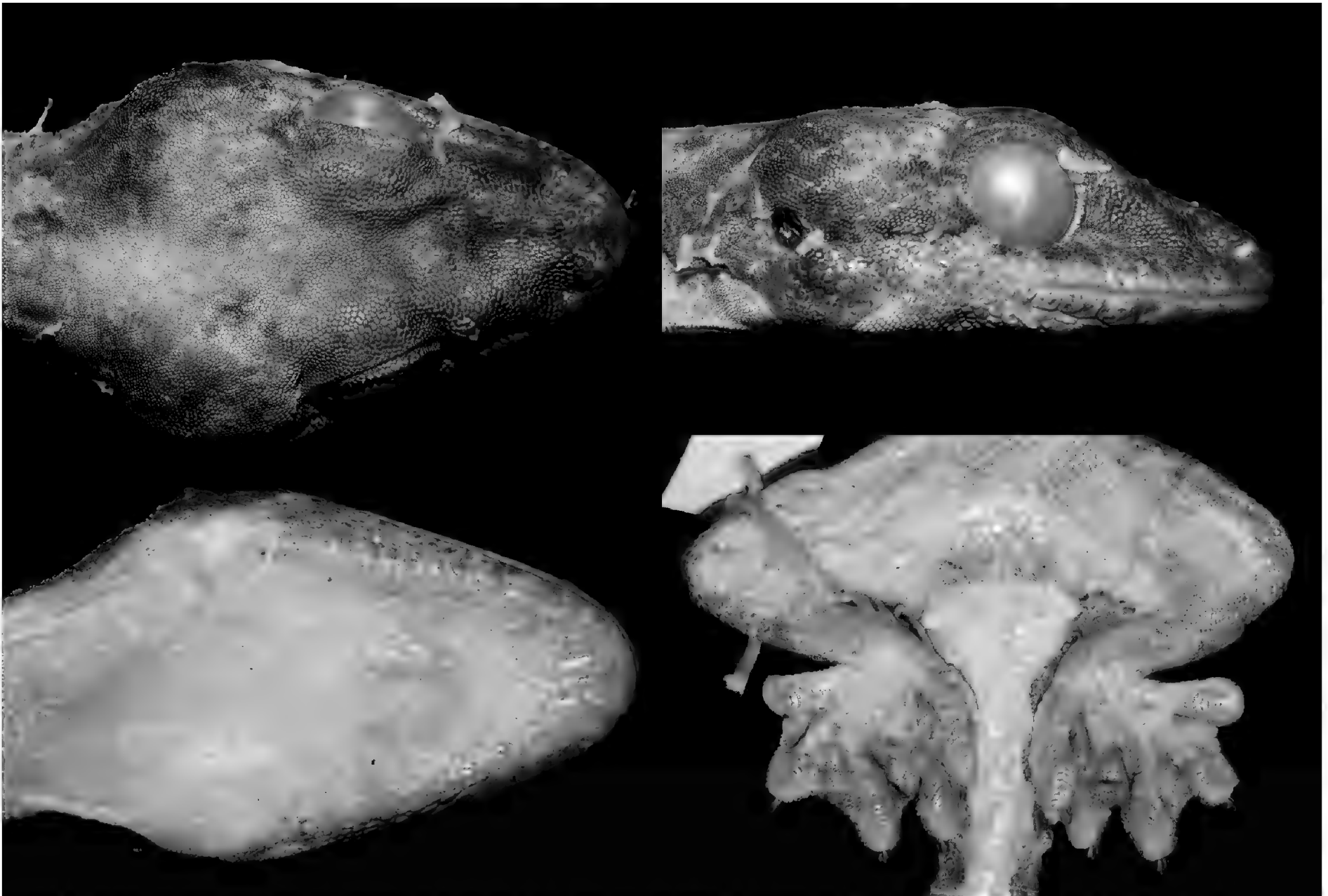


Fig. 6. Dorsal, lateral, and ventral views of the head and ventral view of the feet of *Gekko nicobarensis* (DOSMB05102).

Overall habitus depressed. Supralabials 10–13 and infralabials 10–11 on each side; two moderately enlarged postmentals in broad medial contact, followed by three pairs of scales that are nearly as large as the postmentals. Dorsum bearing four transverse rows of weakly enlarged, rather indistinct tubercles. Ventrals imbricate, in 29–32 transverse rows. Sides of the body bearing a membranous flap of skin, with enlarged, rhomboidal, imbricate scales. A pair of enlarged, rounded cloacal spurs present at the base of the vent. Subcaudals not elongated horizontally, the middle row slightly enlarged. Tail with serrated dermal membranes extending along the sides, forming an oval-shaped disc at the terminus. Tail tip regenerated. Upper arm shorter than lower arm (mean UAL:LAL 0.91); palm enlarged with five fingers; the first one with an indistinct claw; relative lengths of fingers IV>III>V>II>I. Sides of upper and lower arms with extensive skin flaps. Thighs short (mean FEL:SVL 0.18) robust; with a few tuberculated scales on the dorsal surface. Tibia shorter than thighs (mean TBL:SVL 0.16); toes with entire, undivided subdigital lamellae, 14–20 under toe IV; relative lengths of toes IV>III>V>II>I. Tibia bearing lateral flaps of skin. Fingers and toes extensively webbed with membranous skin flaps extending from the base to the tip. Males have a series of 20–21 precloacal pores and lack femoral pores.

Coloration in life. Dorsal coloration variable. Two distinct morphs recorded. One morph with a series of

five or six darker brown ‘W’ shaped transverse bands on the body and five or six similar transverse bands on the tail. The other morph with a bright tan vertebral stripe bordered by darker flanks (Fig. 5). Venter uniform brown and lacking any specific pattern. Eyes with vertically elliptical pupils, a greenish yellow iris and brown reticulations.

Distribution. Occurs on islands of the Northern and central group of the Nicobar Archipelago. Recorded from Car Nicobar, Camorta, Katchall, and Teresa Islands during this study. It has been reported from Chowra, Bompoka, Trinkat, and Nancowry Islands (Das and Vijayakumar 2009) (Fig. 10).

Natural history. Nocturnal in habit. The individuals recorded during this study were observed mostly at a height of approximately 2–2.5 m above the ground on the trunks of relatively short shrubs that were nearly 3–3.5 m tall, with a girth not exceeding 25 cm. Found in primary evergreen forests, also recorded from secondary forests, human habitations, and plantations. Calls of this species could not be heard during the sampling sessions in the field. Pairs of eggs stuck to each other and the tree bark substrate were seen in July.

Remarks. The holotype has 11 supralabials (10–13 in our material), 9 infralabials (10–11), four rows of dorsal tubercles at midbody (4), and 21 subdigital lamellae (14–



Fig. 7. *Gekko stoliczkai* sp. nov. in life from Great Nicobar.

19) under toe IV.

(1999); Vijayakumar (2005) part

***Gekko stoliczkai* sp. nov. (Figs. 7–9)**

Gekko gecko (non Linnaeus, 1758) – Biswas and Sanyal (1977) part

Gekko smithii (non Gray, 1841) – Biswas (1984); Das

[urn:lsid:zoobank.org:act:1795181F-C7AD-4195-A233-2B2F1B13826B](https://zoobank.org/act:1795181F-C7AD-4195-A233-2B2F1B13826B)

Holotype. ZSI/ANRC/T/6092, an adult male collected from Makachua (7.4035°N, 93.7134°E, 37 m asl), Little



Fig. 8. Holotype (ZSI/ANRC/T/6092) of *Gekko stoliczkai* sp. nov. in dorsal (above) and ventral (below) views.

Nicobar Island on 14 August 2018 by G. Gokulakrishnan.

Paratypes. DOSMB05020, an adult female from Shastri Nagar (6.8065°N, 93.8882°E, 41 m asl), ZSI/ANRC/T/6093 an adult female, ZSI/ANRC/T/4796 and ZSI/ANRC/T/7221, two adult males from East-West road (7.0022°N, 93.8811°E, 82 m asl), Great Nicobar.

Etymology. The specific epithet is a patronym honoring Dr. Ferdinand Stoliczka (1838–1874) for his early contributions to the herpetology of Andaman and

Nicobar Islands. Some of his works, such as Stoliczka (1870; 1873), provided significant information on the herpetofauna of the Andaman and Nicobar Islands, which included the description of several new taxa such as *Rana gracilis* var. *andamanensis* (now *Minervarya andamanensis*), *Rana gracilis* var. *nicobariensis* (now *Minervarya nicobariensis*), *Hylorana nicobariensis* (now *Bijurana nicobariensis*), *Typhlops andamanensis* (now *Gerrhopilus andamanensis*), *Ablabes nicobariensis* (now *Gongylosoma nicobariensis*), and *Mococa macrotympanum* (now *Lipinia macrotympanum*).

Table 4. Meristic and morphometric characters of specimens examined for (A) *Gekko verreauxi*, (B) *Gekko nicobarensis*, and (C) *Gekko stoliczkai* **sp. nov.** The specimen number of the new species holotype is in bold.**Table 4A.** Data for *Gekko verreauxi*.

| Species | <i>Gekko verreauxi</i> | <i>Gekko verreauxi</i> | <i>Gekko verreauxi</i> | <i>Gekko verreauxi</i> | Mean |
|-----------------------------|------------------------|------------------------|------------------------|------------------------|--------|
| Catalogue Number: | ZSI/ ANRC/T/3726 | ZSI/ ANRC/T/5779 | ZSI/ ANRC/T/4324 | ZSI/ ANRC/T/4566 | |
| Island | North Andaman | Havelock | South Andaman | Little Andaman | |
| SVL (mm) | 140.06 | 109.55 | 140.62 | 146.49 | 134.18 |
| Trunk length | 67.24 | 41.99 | 69.84 | 66.58 | 61.41 |
| Tail | 93.19 | 105.89 | 142.96 | 127.96 | 117.50 |
| Head length | 33.41 | 31.83 | 36.04 | 38.52 | 34.95 |
| Head width | 25.96 | 27.82 | 32.16 | 31.79 | 29.43 |
| Head depth | 17.14 | 11.31 | 15.89 | 16.96 | 15.33 |
| Eye diameter | 8.84 | 9.11 | 8.02 | 8.29 | 8.57 |
| Tympanum diameter | 4.13 | 4.06 | 3.77 | 4.52 | 4.12 |
| Eye-nostril | 13.69 | 9.87 | 13.04 | 14.17 | 12.69 |
| Eye-snout | 16.18 | 13.86 | 15.88 | 18.66 | 16.15 |
| Eye-tympanum | 11.12 | 10.11 | 12.25 | 13.2 | 11.67 |
| Supalabials | 12 | 12 | 14 | 14 | — |
| Infralabials | 9 | 10 | 11 | 13 | — |
| Post-mentals | 2+4 | 2+4 | 2+4 | 2+4 | — |
| Ventrals | 28 | 27 | 28 | 29 | — |
| Internarial distance | 5.1 | 5.09 | 5.26 | 5.19 | — |
| Upper arm length | 14.35 | 12.31 | 15.53 | 16.23 | 14.61 |
| Lower arm length | 15.62 | 16.03 | 20.76 | 21.56 | 18.49 |
| Palm length | 17.93 | 14.79 | 17.44 | 18.98 | 17.29 |
| Femur length | 18.52 | 18.71 | 25.24 | 24.16 | 21.66 |
| Tibia length | 20.75 | 20.72 | 21.08 | 25.55 | 22.03 |
| Foot length | 16.82 | 17.41 | 21.38 | 21.1 | 19.18 |
| T4 lamellae | 20 | 18 | 20 | 20 | — |
| Sex | M | M | F | F | — |

Table 4B. Data for *Gekko nicobarensis*.

| Species | <i>Gekko nicobarensis</i> | <i>Gekko nicobarensis</i> | <i>Gekko nicobarensis</i> | Mean |
|--------------------------|---------------------------|---------------------------|---------------------------|-------|
| Catalogue Number: | DOSMB05102 | ZSI/ANRC/T/5234 | ZSI/ANRC/T/4235 | |
| Island | Car Nicobar | Teressa | Camorta | |
| SVL (mm) | 91.21 | 95.86 | 78.42 | 88.50 |
| Trunk length | 33.74 | 45.34 | 44.65 | 41.24 |
| Tail | 61 | 63.18 | 61.57 | 61.92 |
| Head length | 25.14 | 27.26 | 22.65 | 25.02 |
| Head width | 17.45 | 20.38 | 18.33 | 18.72 |
| Head depth | 10.07 | 12.7 | 11.02 | 11.26 |
| Eye diameter | 5.55 | 7.13 | 5.76 | 6.15 |
| Tympanum diameter | 1.75 | 3.14 | 2.4 | 2.43 |
| Eye-nostril | 8.21 | 9.13 | 8.91 | 8.75 |
| Eye-snout | 10.54 | 11.94 | 11.54 | 11.34 |
| Eye-tympanum | 7.74 | 8.87 | 6.71 | 7.77 |
| Supalabials | 10 | 13 | 12 | — |
| Infralabials | 10 | 11 | 10 | — |
| Post-mentals | 2+6 | 2+6 | 2+6 | — |

Table 4B (continued). Data for *Gekko nicobarensis*.

| Species | <i>Gekko nicobarensis</i> | <i>Gekko nicobarensis</i> | <i>Gekko nicobarensis</i> | Mean |
|----------------------|---------------------------|---------------------------|---------------------------|-------|
| Ventrals | 29 | 32 | 29 | — |
| Internarial distance | 4 | 4.46 | 3.45 | — |
| Upper arm length | 11.1 | 8.15 | 9.97 | 9.74 |
| Lower arm length | 10.54 | 10.36 | 11.16 | 10.69 |
| Palm length | 10.11 | 9.77 | 8.27 | 9.38 |
| Femur length | 15.74 | 15.8 | 15.1 | 15.55 |
| Tibia length | 14.58 | 15.55 | 13.14 | 14.42 |
| Foot length | 12.97 | 12.92 | 11.88 | 12.59 |
| T4 lamellae | 17 | 14 | 19 | — |
| Sex | F | F | F | — |

Table 4C. Data for *Gekko stoliczkai* sp. nov.

| Species | <i>Gekko stoliczkai</i> sp. nov. | <i>Gekko stoliczkai</i> sp. nov. | <i>Gekko stoliczkai</i> sp. nov. | <i>Gekko stoliczkai</i> sp. nov. | <i>Gekko stoliczkai</i> sp. nov. | Mean |
|----------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|--------|
| Catalogue Number: | ZSI/ANRC/T/6092 | DOSMB05020 | ZSI/ANRC/T/6093 | ZSI/ANRC/T/4796 | ZSI/ANRC/T/7221 | |
| Island | Little Nicobar | Great Nicobar | Great Nicobar | Great Nicobar | Great Nicobar | |
| SVL (mm) | 118.37 | 122 | 123.83 | 128.4 | 116.29 | 121.78 |
| Trunk length | 55.33 | 51.85 | 55.2 | 60.64 | 49.08 | 54.42 |
| Tail | 105.9 | 112 | 130.49 | 81.31 | 103.81 | 106.70 |
| Head length | 32.1 | 31.6 | 30.22 | 36.93 | 30.43 | 32.26 |
| Head width | 24.04 | 23.43 | 21.46 | 25.07 | 23.19 | 23.44 |
| Head depth | 14.17 | 14.28 | 12.93 | 14.54 | 13.69 | 13.92 |
| Eye diameter | 7.84 | 6.76 | 8.05 | 8.66 | 7.68 | 7.80 |
| Tympanum diameter | 4.3 | 3.12 | 3.29 | 3.93 | 2.63 | 3.45 |
| Eye-nostril | 11.77 | 11.16 | 12.15 | 13.94 | 11.54 | 12.11 |
| Eye-snout | 15.04 | 14.05 | 14.95 | 17.15 | 14.51 | 15.14 |
| Eye-tympanum | 10.76 | 9.76 | 10.22 | 11.16 | 9.96 | 10.37 |
| Supalabials | 14 | 14 | 14 | 17 | 15 | — |
| Infralabials | 13 | 12 | 12 | 13 | 12 | — |
| Post-mentals | 2+4 | 2+4 | 2+4 | 2+4 | 2+4 | — |
| Ventrals | 22 | 25 | 23 | 21 | 22 | — |
| Internarial distance | 3.61 | 3 | 4.47 | 4.75 | 4.39 | — |
| Upper arm length | 11.28 | 16.99 | 12.46 | 13.12 | 12.28 | 13.23 |
| Lower arm length | 13.84 | 15.9 | 17.68 | 16.02 | 15.71 | 15.83 |
| Palm length | 15.54 | 16.83 | 12.84 | 16.15 | 11.29 | 14.53 |
| Femur length | 19.91 | 20.96 | 18.88 | 20.96 | 21.15 | 20.37 |
| Tibia length | 18.19 | 20.06 | 17.78 | 18.32 | 16.51 | 18.17 |
| Foot length | 16.08 | 19.85 | 15.53 | 17.28 | 15.91 | 16.93 |
| T4 lamellae | 21 | 22 | 18 | 20 | 21 | — |
| Sex | M | F | F | M | M | — |

Diagnosis. A large-bodied gecko (SVL 116–128.83 mm) restricted to the southern islands of the Nicobar archipelago, characterized by: 14–17 supralabials; 12 or 13 infralabials; two elongate inner pair of postmentals in broad medial contact with each other; two smaller, separated outer pairs of postmentals; 13–15 precloacal pores in males, no femoral pores; two internasals in contact with each other; distinct ventrolateral dermal folds; 21–25 transverse rows of ventrals; 10–12 transverse rows of enlarged, rounded dorsal tubercles; three enlarged post-cloacal spurs on each side of the vent; 18–22 undivided subdigital lamellae under toe IV; presence of five legible, light-colored, creamy white, transverse bands in juveniles, subadults and adults have a pale-white to creamy yellow venter.

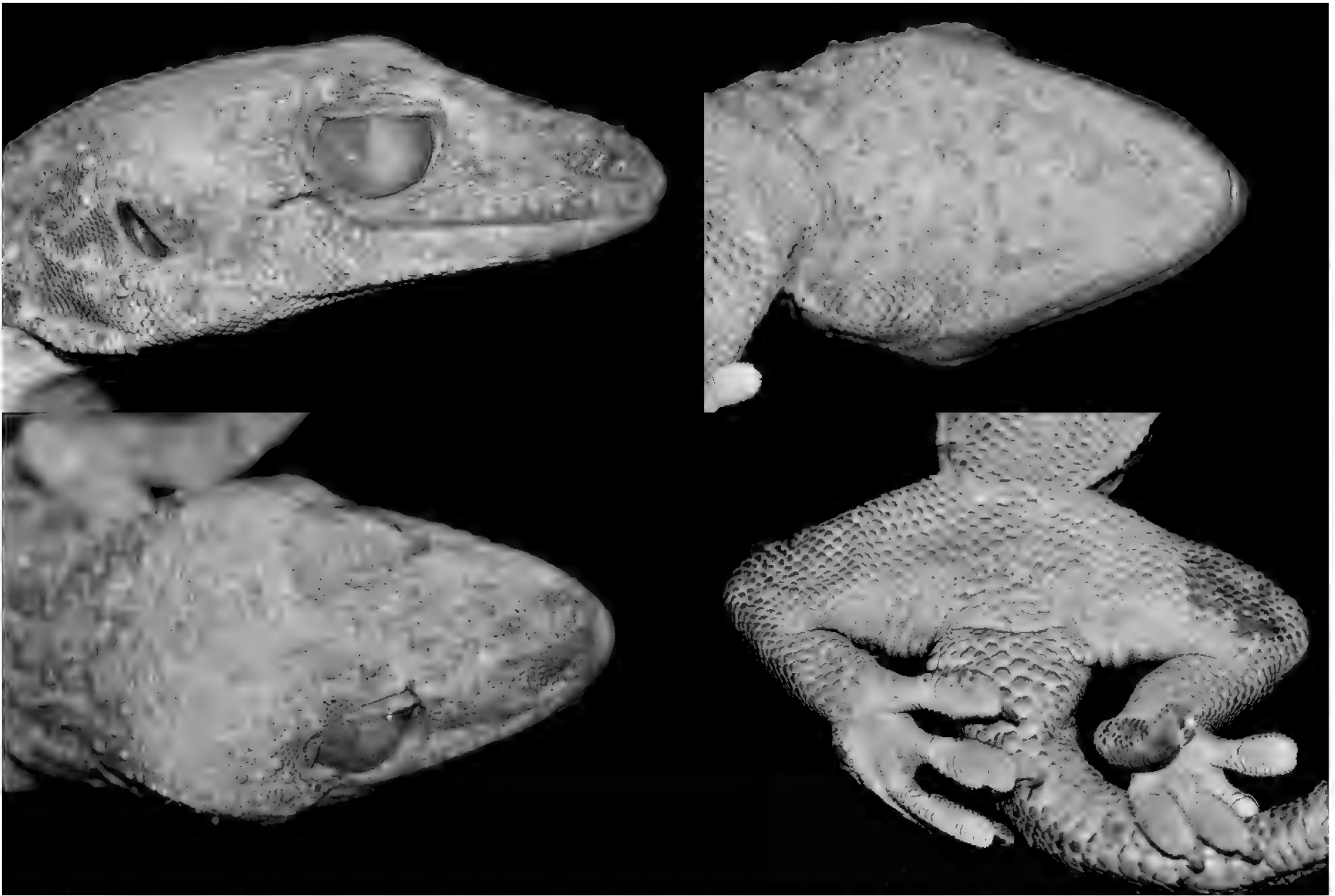


Fig. 9. Lateral, ventral, and dorsal profiles of the head, and precloacal region of the holotype of *Gekko stoliczkai* sp. nov.

Description of the holotype (ZSI/ANRC/T/6092). An adult male, measuring 118.37 mm SVL, head fairly large (HL:SVL 0.27), longer than broad (HL:HW 1.34); with a blunt, rounded snout tip. Eyes fairly large (ED:HL 0.24) with a vertically elliptical pupil; eye slightly smaller than the snout length (ED:ES 0.52); nostrils situated closer to the snout tip than to the eyes (EN:ES 0.78). Trunk slightly shorter than one-half the length of the body (AG:SVL 0.47). Overall habitus depressed. Supralabials 14 on each side, infralabials 13 on each side; two moderately enlarged postmentals in broad medial contact, followed by two pairs of enlarged scales, that are nearly as large as the post-mentals. Dorsum bearing 11 transverse rows of enlarged, rounded tubercles. Ventrals imbricate, in 22 transverse rows. Two pairs of enlarged, rounded cloacal spurs present at the base of the vent on each side. Subcaudals horizontally elongate, the mid-anterior scales not enlarged. Tail slightly shorter than the body (SVL:TAL 1.12). Upper arm shorter than lower arm (UAL:LAL 0.82); palm with enlarged, undivided subdigital lamellae; the first one with an indistinct claw; relative lengths of fingers IV>III>V>II>I. Thighs short (FEL:SVL 0.17) and robust; with a few tubercles on the dorsal surface. Tibia shorter than thighs (TBL:SVL 0.15); toes with entire, undivided subdigital lamellae, 21 on toe IV; relative lengths of toes IV>III>V>II>I. Fifteen undivided series of precloacal pores; the pore-bearing scales relatively smaller than those above. Fingers and toes free, lacking membranous skin flaps.

Coloration. In life, overall ground coloration dull-brown with five or six indistinct pale-white transverse cross-bars on the body. Tail regenerated and uniform brown. Venter brown with small brown spots on each ventral scale. Eyes with vertically elliptical pupils and a bluish iris. In preservation, the dorsal coloration faded to a near-uniform dull brown with a pale white venter. The transverse bars barely visible and the bluish coloration of the iris faded.

Variation. Measurements and scale counts of the paratypes are given in Table 4. Females lack precloacal pores and are nearly as large as males. Light-colored, creamy white, transverse bands are more legible in juveniles and subadults while the adults usually have feeble dorsal bands. Ventral color ranges from pale-white to creamy yellow.

Natural history. Nocturnal and found in a variety of habitats ranging from evergreen forests, semi-evergreen forests, and plantations to human habitations. Frequently observed on walls of buildings, or on tree trunks of tall trees at heights ranging from about 6 to 13 feet. Calls comprise a series of repeatedly uttered, interrupted rattling syllables of *tuk...tuk...tuk...tuk* advancing into high frequency syllables of *tuk-tuk-tuk-tuk* (also see Biswas 1984).

Comparisons. *Gekko stoliczkai* sp. nov. can be

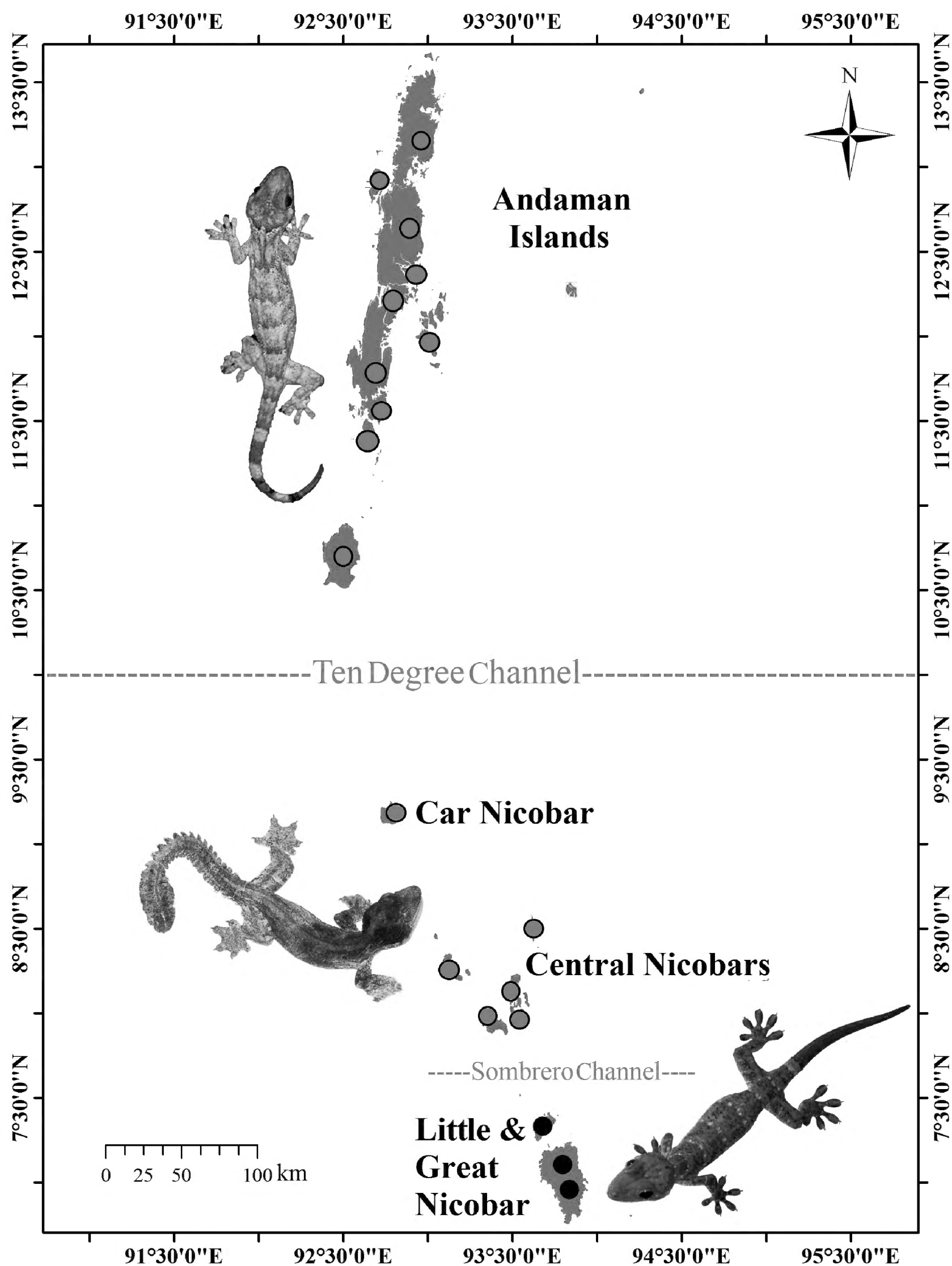


Fig. 10. Map of the Andaman and Nicobar Islands showing the distributions of *Gekko verreauxi* (red), *Gekko nicobarensis* (yellow), and *Gekko stoliczkai* **sp. nov.** (black).

differentiated from *G. smithii* by having significantly fewer numbers of internasals and ventrals and having significantly higher numbers of infralabials and supralabials (Tables 1–3; Figs. 1–2). It can be further separated from *G. smithii* by its less gracile more stout body features, in having a significantly narrower and shorter head and snout, a significantly smaller orbit,

and significantly shorter limbs and trunk. From *G. verreauxi*, it is differentiated by the separation of nasal and rostral scales (vs. in contact in *G. verreauxi*), bluish iris (vs. greenish in *G. verreauxi*), and greater number of supralabials (14–17 in *G. stoliczkai* **sp. nov.** vs. 12–14 in *G. verreauxi*). From *Gekko nicobarensis*, *G. stoliczkai* **sp. nov.** can easily be distinguished by the absence of skin-

flaps along the sides of the body and tail, and extensive webbing between fingers and toes (vs. present in *G. nicobarensis*), and by the separation of nasal and rostral scales (vs. in contact in *G. nicobarensis*). Additionally, from other members of the *Gekko gekko* group, the new species *G. stoliczkai* **sp. nov.** could be distinguished as follows (only opposing suite of characters mentioned): *G. albofasciatus* (16 precloacal pores and reddish olive dorsal coloration), *G. gekko* (11–15 supralabials; gray to bluish or brownish dorsal color with reddish spots), *G. mutaphandi* (12–14 supralabials; 17–22 precloacal pores in males; 15 subdigital lamellae under toe IV), *G. reevesii* (10–14 supralabials; 13–20 precloacal pores; gray-green to dark grey dorsal coloration), and *G. siamensis* (13–21 supralabials; 10–13 precloacal pores; grey-brown to dark green dorsal coloration) *fide* Rösler et al. (2011).

Distribution. Recorded during the present study from Great and Little Nicobar Islands. It has been reported from other smaller islands such as Pigeon, Pilo Milo, Menchal, and Kondul in the southern group of the Nicobar Islands (Vijayakumar 2005) (Fig. 10).

Discussion

A fairly recent taxonomic review of the genus *Gekko* by Rösler et al. (2011) defined six species groups based on morphological and phylogenetic evidence and classified the members that formed six sub-clades. As per their scheme of classification, *Gekko smithii* and *G. verreauxi* fall under the *Gekko gekko* group, among which, *G. smithii* was shown to comprise a complex of several populations within the Sundaland. The subsequent classification of this group under the subgenus *Gekko* by Wood et al. (2019) is in agreement with that of Rösler et al. (2011). Although Das (1999) doubted that the Nicobar population of *G. smithii* was potentially allied to an undescribed member of this group from Sumatra and specifically distinct from the nominate species, *Gekko smithii*, no taxonomic assessments of this population have been made until now, despite several of the earlier field-based observations, collections, and records (Biswas and Sanyal 1977; Vijayakumar 2005; Harikrishnan et al. 2014). The present study has filled in this long-standing lacuna by providing taxonomic clarity for the Nicobarese population. A report of the ‘presence’ of *Gekko smithii* from Camorta in the central Nicobar Islands by Harikrishnan et al. (2014: 18) is erroneous and it does not occur there (pers. obs.).

Additionally, this study provides new data on the other poorly-known members of the genus *Gekko* found in the Andaman and Nicobar Islands, especially *G. verreauxi*, which is restricted to the Andaman archipelago. Although earlier studies provided some information on taxonomy and field observations (Ota et al. 1991; Veselý 1999), this species has remained poorly known until now. Mohan et al. (2020) studied

intraspecific genetic variation within *G. verreauxi* across the Andaman Islands and found it to be low, implying a genetic uniformity across the island populations, as expected (e.g., as in *Phelsuma andamanensis* and *Cyrtodactylus rubidus*). The other species, *Gekko (Ptychozoon) nicobarensis* was variously attributed to *Ptychozoon homalocephalum* and *Ptychozoon kuhli* historically (Stindachner 1867), until Das and Vijayakumar (2009) identified this population to be specifically distinct, thereby conferring it the name *Ptychozoon nicobarensis*. They diagnosed the species based on ‘dorsum with tan vertebral stripe, lacking dark transverse bars’ (Das and Vijayakumar 2009: 10). Their description was based on a commendable series of 20 specimens, comprising seven males and 13 females. However, our new material for this species indicates that it is much more variable in morphology and color pattern than previously ascertained, and can have either a striped or banded dorsal pattern (Fig. 3). The Andaman Islands are separated from the Nicobar Islands by the Ten-Degree Channel, which acts as an effective biogeographic barrier, limiting the distribution of *G. verreauxi*. Likewise, the Sombrero Channel running between the central and southern groups of Nicobar Islands act as a barrier in limiting the distributions of *G. nicobarensis* and *G. stoliczkai* **sp. nov.** The Great Channel, running between Great Nicobar and Sumatra, acts as a biogeographic barrier which separates the distribution ranges of *G. stoliczkai* **sp. nov.** (Southern Nicobar Islands) and the Sundaic Island of Sumatra, occupied by *Gekko smithii*. Among these, the conservation status has been assessed only for ‘*G. smithii*’ as Least Concern. Considering the relatively wide geographic distribution and fairly high abundance (pers. obs.), we recommend *G. verreauxi* to be classified under the Least Concern category, while the other two species, *G. (P.) nicobarensis* and *Gekko stoliczkai* **sp. nov.**, with their distribution ranges restricted to a few relatively smaller islands, would fall under the Endangered category, owing to their much narrower geographic distributions.

Acknowledgements.—We thank the Department of Environment and Forests, Andaman and Nicobar Islands for permission (permit numbers: CWLW/WL/134/(J)/Folder/417 and CWLW/WL/134 (L)/ 60) allowing SRC to conduct this study and for the infrastructure provided. SRC is thankful to the Mohamed bin Zayed Species Conservation Fund for grants (#14058387 and #160514249) which partly facilitated this study. We thank the faculty of the Department of Ecology and Environmental Sciences and the Department of Ocean Studies and Marine Biology, Pondicherry University, for the lab space and support extended. CS and GG thank Kailash Chandra, Director, Zoological Survey of India, Kolkata, for his support, cooperation, and encouragement during the survey.

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L. Lee Grismer studies phylogeny, taxonomy, biogeography, and character evolution in amphibians and reptiles from Southeast Asia. Lee has been working throughout the region for over 25 years, and he has contributed significantly towards studies on the systematics of the Oriental gekkonid genus *Cyrtodactylus*.

Appendix 1. Comparative material of *Gekko smithii* examined.

Peninsular Malaysia: LSUHC 3891, LSUHC 3990, LSUHC 4681, LSUHC 4694, LSUHC 4697, LSUHC 5059, LSUHC 5060, LSUHC 5061, LSUHC 5062, LSUHC 5063, LSUHC 5151, LSUHC 5152, LSUHC 5390, LSUHC 5399, LSUHC 5849, LSUHC 6260, LSUHC 6265, LSUHC 6277, LSUHC 6278, LSUHC 6282, LSUHC 6283, LSUHC 6284, LSUHC 6542, LSUHC 6564, LSUHC 6606, LSUHC 6890, LSUHC 7024, LSUHC 7025, LSUHC 7026, LSUHC 7251, LSUHC 7257, LSUHC 7263, LSUHC 7264, LSUHC 7299, LSUHC 7648, LSUHC 7649, LSUHC 7650, LSUHC 7651, LSUHC 7694, LSUHC 7702, LSUHC 9153, LSUHC 9154, LSUHC 9155, LSUHC 9156, LSUHC 9157, LSUHC 9158, LSUHC 9626, LSUHC 9959, LSUHC 10585, LSUHC 10596, LSUHC 11976, LSUHC 11977, LSUHC 12028, LSUHC 13476, LSUHC 13624, LSUHC 13625, LSUHC 13626, LSUHC 13627, LSUHC 15041, LSUHC 15042, LSUHC 15052, LSUHC 15053, LSUHC 185107, LSUHC 185112, LSUHC 185113, LSUHC 185119, LSUHC 185126, LSUHC 185135, LSUHC 185136, LSUHC 185139, LSUHC 185141, LSUHC 185142, LSUHC 185144, FMNH 185145, FMNH 185114, FMNH 185120.

Thailand: THMNH 1841, THMNH 1844, THMNH 3247, THMNH 11432, THMNH 13910.

Sumatra: FMNH 209498–503, USNM 29396, USNM 197804; MVZ 21122–25; ZMA 17947A–B, 17952.

Borneo: FMNH 128893–95, FMNH 129492, FMNH 129495–96, FMNH 131520–22, FMNH 230176, 246237–28, 248986; ZRC 2.5302, ZRC 2.5691, ZRC 2.5704, 2.1488.